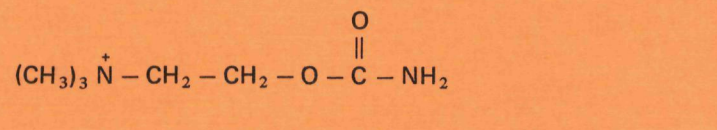
INFORMATION-STATISTICAL ANALYSIS OF SOCIAL INTERACTION IN JAVA-MONKEYS

applied in

THE NEURO-ETHOLOGY OF THE CAUDATE NUCLEUS



$$T_{I_{t-1}}(I_t : J_{t-1}) = H(I_t\, I_{t-1}) + H(I_{t-1}\, J_{t-1}) - H(I_{t-1}) - H(I_t\, I_{t-1}\, J_{t-1})$$

John van den Bercken

INFORMATION-STATISTICAL ANALYSIS OF SOCIAL INTERACTION IN JAVA-MONKEYS

applied in

THE NEURO-ETHOLOGY OF THE CAUDATE NUCLEUS

PROMOTORES: PROF.DR. E.E.CH.I. ROSKAM
PROF.DR. J.M. VAN ROSSUM

COREFERENT: DR. A.R. COOLS

INFORMATION-STATISTICAL ANALYSIS OF SOCIAL INTERACTION IN JAVA-MONKEYS

applied in

THE NEURO-ETHOLOGY OF THE CAUDATE NUCLEUS

Proefschrift

ter verkrijging van de graad van doctor in de sociale wetenschappen aan de Katholieke Universiteit te Nijmegen, op gezag van de rector magnificus Prof.Dr. P.G.A.B. Wijdeveld volgens besluit van het college van decanen in het openbaar te verdedigen op donderdag 6 december 1979 des namiddags te 2.00 uur precies

door

Johannes Hermanus Ludovicus van den Bercken

geboren te Horst

1979
Krips Repro B.V.
Meppel

CONTENTS

The investigations were carried out at the Department of Pharmacology of the University of Nijmegen; the work was supported in part by the Foundation for Fundamental Biological Research (BION), which is subsidized by the Netherlands Organization for the Advancement of Pure Research (ZWO).

x

CHAPTER 1

GENERAL INTRODUCTION

This thesis presents some work on the analysis of social interaction in Java-monkeys, in the context of neuro-ethological research into the caudate nucleus of the brain. The general paradigm for neuro-ethological research is to experiment on the brain of an animal and to study its behaviour by ethological methods. In our experiments, the caudate nucleus of the brain is treated by injection of small amounts of the cholinergic drugs carbachol and atropine. The dependent variable is the sequential structure of behaviour, in particular, the way in which the current behaviour of a treated monkey is influenced by its immediately preceding behaviour and that of its partners. The first problem to be dealt with is, therefore, how the organization of ongoing behaviour (of Java-monkeys) in a social situation can be described and analysed. The second problem is how the effects of pharmacological treatment of the caudate nucleus can be interpreted in terms of the sequential structure of ongoing behaviour.

Preliminary to the analysis of social interaction is the task of the empirical identification and description of the social behaviour of the species under study. This amounts to establishing as complete and detailed an inventory of behaviour as possible. It is difficult to make a sharp and consistent distinction between the notions of behaviour in general and social or communicative behaviour in particular. In the context of primate communication, for instance, Carpenter (1969) considers social behaviour to be "more general" and communicative behaviour "more specific and limited", and "more economical of energy and effort". According to Bastian (1965) however, "we have no basis for restricting com-

munıcatıve actıons to anythıng less than the whole of socıal behavıour".

Characteristic for communication is not the occurrence of a particular class of behaviour patterns, but rather the occurrence of a particular effect of behaviour. Communication usually refers to constraints on individual behaviour resulting from the behaviour of others. "Can either communication or social behaviour be considered as anything other than the partial and often reciprocal determination of the actions of one or more individuals by the actions of one or more others?" (Bastian, 1965). Altmann was the first to employ this notion of communication. "When we say that, in a communicative process, the behaviour of one individual affects the behaviour of another, we mean that it changes the probability distribution of the other." (Altmann, 1967). The effect of communication, or the fact that one individual affects the behaviour of another, may therefore be studied by relating the preceding behaviour of one individual (henceforth denoted as "partner") to the probability of response in another individual (henceforth denoted as "reference subject"). We will follow the approach initiated by Altmann and define the occurrence of social interaction and communication in terms of the associations that occur between the behaviour sequences of a number of individuals ("interaction sequences" for short).

The approach of Altmann therefore circumvents the need to demarcate a special subset of behaviours as being "social" or "communicative". When several individuals, e.g. monkeys, live together, the situation is by definition social and all behaviour patterns are potentially communicative. Moreover, the definition advocated by Altmann already embodies a proposal for quantitatively studying some aspects of the behavioural consequences of communication. We will extend this idea and incorporate it into a formal model for studying communication as one factor determining behaviour in a social situation. In short it may be stated as follows: - the sequencing of behaviour patterns in a social situation is the result of obeying two simultaneous demands: realization of individual goals and adaptation to external vicissitudes, in particular the behaviour of others. The model is developed in order to

determine the effect of these factors in the structure of observed behaviour sequences. The effects are identified as the influences on the ongoing behaviour of a reference subject, stemming from the previous behaviour of the reference subject itself and from that of its partners; the latter effect is taken to represent "communication".

The model is formulated by means of information-theoretical statistics. The reason for using information theory is mainly the fact that its formalism is very well suited to the kind of data usually obtained in ethological research, especially nominal data such as behaviour sequences. Moreover, in the ethological literature on the analysis of social behaviour several information statistical models have already been proposed. These models will be discussed and compared with our model.

The subjects discussed up to this point constitute the ethological and data-analytical part of this thesis. In chapter 2 we discuss the currently available descriptions of the behaviour of Java-monkeys, the species that was used in our work. The technical equipment used for the observation of the behaviour of the monkeys in our experimental situation is described in chapter 3. In chapter 4 our information-statistical model for analysing the factors determining ongoing behaviour is presented, while chapter 5 reviews earlier information-statistical models for the analysis of social interaction. An empirical comparison of the models outlined in chapters 4 and 5 is given in chapter 6 by applying each model to the same set of data. In chapter 7 our model (from chapter 4) is applied to the analysis of particular aspects of communication between monkeys and for the measurement of dominance as relevant to group structure. Finally, as interaction sequences are just a special type of multivariate categorical data, some general computational and statistical problems associated with the information-theoretical analysis of such data are discussed in chapter 8 (note that there are other varieties of analysis of multivariate categorical data, e.g. the approaches developed by Benzécri* and by Hayashi**).

---

*Benzécri, J.P. (1973) L'Analyse des Données, Tome I et II. Dunod, Paris.

The final three chapters are concerned with the neurobehavioural part of the work reported on. In chapter 9 the neurobiological literature on the caudate nucleus is briefly reviewed and the hypothesis to be investigated in the following two chapters is outlined.

The general problem in research on brain-behaviour relationships is to show that particular brain areas are substrates of particular behaviours or categories of behaviour, e.g. aggression (Perachio and Alexander, 1975) or affiliative behaviour (Kling and Steklis, 1976). Two types of statement are commonly found: that many brain structures are involved in the control of one single category of behaviour (e.g. the hypothalamus, amygdala, septum etc. in aggression), and that one structure is involved in many kinds of behaviour (e.g. the hypothalamus in eating, sexual activity etc.). Such conclusions often presuppose a rather crude concept of cerebral organization and localization of function (Webster, 1973; Zülch, 1976) and are based on a relatively haphazard accumulation of empirical data, since many investigators focus on just one class of behaviour. Another flaw in brain-behaviour research is the lack of sophistication with respect to the behaviour or behavioural process under study. In the ethological part of this thesis we have taken great care to outline some aspects of the sequential organization of ongoing behaviour.

In chapter 10 the effects of the cholinergic drugs carbachol and atropine, injected into the caudate nucleus, on the sequential structure of behaviour is investigated. The injections were administered by means of a telestimulation technique, so that during the experiments the stimulated monkey could move around freely and engage in all kinds of interaction with other monkeys. In chapter 11 the effects of the same drugs applied to the caudate

---

**Hayashi, Ch. (1978) Comparison of two types of multidimensional scaling methods - Minimum dimension analysis MDA-OR and MDA-UO. Annals of the Institute of Statistical Mathematics, Vol. 30, part B, pp. 199-209.

nucleus are evaluated in terms of the occurrence of behaviour patterns of different ethologically defined categories or motivational systems, in order to establish the specificity of the effects with respect to the aspect of the behaviour affected. In order to establish specificity with respect to the brain structure involved, the effect of applying cholinergic drugs to the amygdala are also investigated in chapter 11. It will be shown that the caudate nucleus is not involved in the control of particular categories of behaviour, but in a type of higher-order control, governing the relationships between successively occurring behaviour patterns.

CHAPTER 2

THE ETHOGRAM OF MACACA FASCICULARIS

In the early sixties ethologists started to describe the behaviour of macaques in a systematic way, particularly in the context of the study of animal communication (Altmann, 1967). The favourite species was the rhesus monkey (macaca mulatta: Altmann, 1962; Hinde and Rowell, 1962; Rowell and Hinde, 1962). Other species soon followed: Java-monkeys (Macaca fascicularis: Goustard, 1963; Shirek-Ellefson, 1967; Angst, 1974; De Waal et al., 1976) and stumptail monkeys (Macaca arctoides: Bertrand, 1969; Chevalier-Skolnikoff, 1974). As the number of species under study increased, comparative investigations were undertaken, focusing on facial expression in primates as an important subset of social behaviour (Van Hooff, 1967; Chevalier-Skolnikoff, 1973; Redican, 1975). Along with the growing number of studies, however, confusion arose over matters of terminology and definition. An illustrative example of this situation is provided by Reynolds (1976) who tried to establish the correspondence between several independently developed ethograms of the rhesus monkey. He identified 24 types of social behaviour that were present in each ethogram; even these 24 items did not always have the same label. Large quantities of data from each catalogue could not be matched (the largest ethogram consisted of more than 120 items!).

The following discussion will be concerned with the ethogram of Java-monkeys only. The social organization of this species has been studied in various situations, from fully free-ranging colonies, captive groups living in a restricted area, to small laboratory groups (Goustard, 1961; Furuya, 1965; Thompson, 1967, 1969; Sockza, 1973; Poirier and Smith, 1974; Angst, 1975;

Hendricks et al., 1975). The first systematic inventory of the social behaviour of macaca fascicularis was provided by Angst (1974), working at Basel Zoo. At about the same time laboratory groups were established by Timmermans in Nijmegen and by Van Hooff in Utrecht. These groups offered the opportunity to verify and extend the data from the literature.

In this chapter I will first describe some general strategies used in defining behaviour patterns. Next, I will briefly indicate how the existing descriptions of Java-monkey behaviour have been construed and then present the definitions used in the work to be reported upon in the remainder of this thesis. During that work some critical considerations on the methodology of constructing an ethogram took shape which ultimately led to an alternative approach in describing ongoing behaviour. Although this new approach is not applied in this thesis, it seems appropriate to present it briefly, together with the considerations that gave rise to it.

APPROACHES IN DEFINING BEHAVIOUR PATTERNS

"Behaviour pattern" usually refers to the state of affairs resulting from any observable change in the spatio-temporal configuration constituted by an animal and its immediate surroundings (Hutt and Hutt, 1970). It does not matter at this point whether the observed changes are described in terms of relationships between various effector activities or in terms of relationships between the animal and states of the environment. For an observer any change in the stimulus pattern represented by the animal and its surroundings will qualify as behaviour (if it is brought about by the animal itself).

The kind of work involved in constructing an ethogram has neatly been summarized by Hinde (1970): "The task of the taxonomist of species is to sort out the almost unlimited diversity of individuals in nature into easily recognizable groups, to describe those groups in terms of their significant characters, and to define the differences among them. Similarly, a complex stream of behaviour must be described and broken down into units suitable for study,

which then must be classified into groups according to common properties. No two units will be absolutely identical in all of their properties....." This programme does not however contain much practical guidelines. According to Eibl-Eibesfeldt (1970) the construction of a precise catalogue of all the behaviour patterns of an animal is a rather straightforward business: "For this catalogue one selects functional units of behaviour which are neither too small nor too large. In practice it is not too difficult to find such easily recognizable functional units which are constant in form, such as scratching, chewing, and head-up tail-up." It may be not too difficult indeed for an individual observer to define a workable ethogram; the communication of such definitions to other people is however not very easy. As Reynolds (1976) points out, there are many factors causing differences in the descriptions offered by different authors. "The ways monkeys behave have, it seems, many properties, different ones of which are selected by different observers as the basis for naming them. Structure, function, motivation and context may, for instance, be selected."

Subset specification

In general, two conceptually different approaches have been used in defining behaviour patterns. The first method may be called "identification by subset specification". It presupposes a set of elementary states, $E = \{ e_i \mid i = 1 \ldots m \}$; some of them, but not necessarily all, may occur simultaneously. A behaviour pattern is constituted by a subset of E. The elements that make up a behaviour pattern, are perceptual primitives (Gestalts); their perceptual unity corresponds to the physical unity of the effector systems showing particular states (ear movements, arm movements, turning round etc.). Some terminology may be useful. A "defining" element is an element that is necessary and sufficient for an observer to state that behaviour pattern X is present at a particular time. A "differential" element is an element that is necessary and sufficient for establishing a difference between behaviour patterns X and Y. Defining elements identify behaviour patterns as "the same"; differential elements identify behaviour patterns

as "different". (The distinction between differential and defining elements is analogous to Altmann's distinction between "criteria of sequential demarcation" and "criteria of membership", Altmann, 1967). Another kind of element are the optional elements: these may occur in a particular behaviour pattern, but are not necessary for identification; optional elements can be regarded as background variation. To summarize: a behaviour pattern consists of one or more defining elements; one or more optional elements may be added; some of the defining elements may be differential elements for that pattern. Somewhat related is the method of "cluster concepts" (see Purton, 1978). Cluster concepts can be interpreted as a special case of definition by subset specification. In this case each of the elements in E is a defining property, but not all of them are necessary for identifying the concept; any subset of E (of a certain minimum size) defines the same concept. This procedure appears to be useful for defining functionally equivalent patterns, i.e. patterns having the same consequences.

Vector specification

The second method for defining behaviour patterns may be called "vector specification". In this case a set of elementary subsystems or variables is presupposed. The behaviour pattern is specified as a vector variable by listing the value or state of each component. The difference between the subset specification and the vector specification methods lies in the number of elements entering in the definition of the pattern. In vector specification the same set of elements is checked for each pattern; patterns are different when at least one of the elements has a different value in each pattern. In subset specification a behaviour pattern may be composed of a highly variable number of elements. Subset definitions reflect more interpretative activity of the observer; only those elementary states that are thought to be relevant enter the definition of a behaviour pattern. In vector specification each of the elements is given equal weight. Patterns specified by subset enumeration can be regarded as intuitively defined equivalence classes over the points in the space spanned

by the components used in the vector specification approach. The difference between defining behaviour patterns by subset specification or by vector specification has an important practical consequence. A behaviour pattern identified by a variable number of constituting elements is usually interpreted as one single state and, accordingly, described by means of one single code. A behaviour pattern specified by a fixed number of elements is by definition coded as a vector variable.

Syntactical specification

As will be illustrated below the method of subset specification is attractive because it provides a manageable ethogram, of a convenient size and easy to code, but not very detailed. The method of vector specification nicely preserves the structure of compound behaviour patterns but tends to become unwieldy. An intermediate approach seems to be possible by describing each behavioural state or activity pattern by means of a syntactical formula. Single behaviour states can be represented by one code and codes for simultaneously occurring states can be combined according to a simple generative syntax. We developed such a procedure while working with an ethogram based on subset specification, after we found out an ethogram based on vector specification was too complex. It will be discussed in more detail in the last section of this chapter.

DESCRIPTIONS OF JAVA-MONKEY BEHAVIOUR

Shirek-Ellefson

In practice it is not easy to define the approach of the existing descriptions unambiguously. Shirek-Ellefson (1967) is the best representative of the vector specification method, but her work is restricted to facial expressions. She borrows the concept of expressive element from Van Hooff (1962). "An expressive element is an anatomical feature, such as the ears, eyes, mouth, in a given posture, i.e. open, closed, forward, etc." (p. 43). "Visual communication patterns can be described by listing expressive elements..... Each recurring cluster of elements is unique and makes

a unique visual pattern, so that in a verbal description only one expressive element may differ and yet the total character of the cluster in question is unmistakably unique." (p. 44). As an example, let us take the description of the "open-mouth threat". "When all the expressive elements of an open-mouth threat are present, it consists of: 1) mouth open, 2) mouth corners drawn back to the first molar, 3) lips are tense and pressed against the teeth and retracted vertically slightly, thus exposing the tips of the canine teeth, 4) head lowered so that the crowns of the lower molars are visible, 5) eyes open wide and staring at the receiver, 6) eyebrows retracted slightly, and in combination with the widely opened eyes an encirclement of white skin is exposed around the eyes, 7) ears pulled forward so that they stick out at the sides of the head; in combination with brow retraction, the frontalis muscle is bunched up on the forehead, 8) hair on the top of the head and shoulders is erected, 9) body rigid, and if there is a movement it is forward in decisive steps that can turn into running; ground slapping occasionally occurs, especially when the animal is sitting rather than standing, 10) a roar accompanies this pattern (.....). In its mildest form an open-mouth threat consists of a stare with the slightest indication that the ears are moving forward. This combination of elements presents the sender's staring eyes, its mouth and teeth, and its shoulders. The body movement and the facial expression grade into chasing and biting." (pp. 45-48).

Angst; Welling

Angst (1974) uses the method of subset specification. He defines 104 "Ausdruckselemente" and uses them to describe 76 "Ausdrucksleistungen" or expressive behaviours. Any of the 76 behaviour patterns is defined as a subset of the collection of 104 behavioural elements. Ten behaviour patterns are constituted by just one element; twenty behaviour patterns consist of one defining element and one optional element. The remaining behaviour patterns are more complex. His description of Shirek-Ellefson's "open-mouth threat" runs as follows. "Elemente: Fixieren, Vorstrecken des Kopfes, Mundaufsperren: der Mund wird aufgesperrt, die Lippen-

muskulatur erscheint schlaff, denn die Zähne sind entsprechend dem Grad der Mundöffnung verdeckt oder leicht entblöszt. Ohrenspreizen: Die Ohren werden abgespreizt. Brauen-heben: Hochziehen der Augenbrauen und damit Vorzeigen des weiszlichen Feldes zwischen Auge und Augenbraue. - Beim Stummen Drohen werden oft die Nackenhaare gesträubt. Zudem lassen sich beträchtliche individuelle Unterschiede beobachten." (Angst, 1974, p. 17). The pattern described is called "Stummes Drohen". A related pattern is "Drohen mit Grunzen", described as follows: "Elemente: Alle Elemente des Stummen Drohens, nur Mundaufsperren is ersetzt durch Grunzen. Drohgrunzen: Stimmhaftes "rrrr" von meist nahezu einer halben Sekunde Dauer. Die Mundspalte is dabei nur schwach geöffnet. Die Tendenz zum Tiefhalten des Kopfes is hier weniger ausgeprägt als beim Stummen Drohen." (p. 18). Thus, "Stummes Drohen" is defined by the presence of the elements "Fixieren", "Vorstrecken des Kopfes", "Mundaufsperren", "Ohrenspreizen" and "Brauenheben". "Mundaufsperren" differentiates the pattern from "Drohen mit Grunzen". The element "Fellsträuben" is an optional element. Another example: the behaviour pattern "Imponierendes Anvisieren" consists of the following elements: "Fixieren", "Vorstrecken des Kopfes", "Ohrenanlegen", "Imponierendes Schwanzaufrichten" and "Zurückziehen der Kopfhaut". The pattern "Sexuelles Anvisieren", however, is defined by almost the same subset of elements, only the element "Imponierendes Schwanzaufrichten" is not present in "Sexuelles Anvisieren"; this element is therefore a differential element.

A more global kind of subset specification is found in Welling's descriptions (1977). The patterns are specified by listing a number of behavioural elements or simple effector activities. However, no separately defined collection of elements is presented. The description of "Threatening" is as follows (it is explicitly identified as what Angst labelled "Stummes Drohen" and "Drohen mit Grunzen"): "The eyes are widely opened and directed at the partner, the head is moved forward and sometimes slightly lowered. The eye brows are usually retracted in such a way that the area between the eyes and the eye brows, which is more or less white, becomes visible. The mouth is opened slightly

or widely, the lips are not tense and are usually completely covering the teeth. Sometimes the hair is raised. There are many individual variations. Threatening without vocalization is the most common type of the patterns. In "Threatening and grunting" the mouth is only slightly opened and the animal emits a noise which sounds like "rrr" and has a duration of about half a second." (p. 25).

De Waal

From the examples presented so far it will be evident that a more economical way to identify behaviour patterns is to concentrate on the differentiating elements. Although other defining elements are not optional, as they invariably occur together with the differential elements, they can be considered to be coincidental, as mere covariables accompanying the differential elements. This strategy appears to have been used by De Waal et al. (1976). Behaviour patterns become therefore virtually identical with a constituent element. This is the limiting case for subset specification.

The resulting descriptions can be used in cluster concepts for broader behaviour patterns. For instance, the occurrence of "threat" is defined by the presence of at least one of the following facial expressions, vocalizations and intention movements: "1) Staring: fixedly looking at partner (....). 2) Open-mouth: staring with opened mouth (....). 3) Grunt: simple and rather soft vocalization; "hur" (....). 4) Head-bob: nodding head down- and forewards (....). 6) Ground-slap: slapping on the ground with hands (....)." (pp. 261-262). It should be noted that this approach will only work well if elements such as 1 to 6 in this example cannot occur simultaneously. This point will be taken up in the section on methodological considerations.

The foregoing examples merely serve as an illustration of the ways in which behaviour patterns have been identified. I will not endeavour to make a detailed comparison of the definitions given by the various authors. In many instances such comparisons are provided by the authors themselves by references to the definitions of others.

AN INVENTORY OF BEHAVIOUR PATTERNS IN JAVA-MONKEYS

In the following list the descriptions are preceded by the numbers that were actually used in coding the observed behaviour sequences. They also indicate the relative priority of the behaviour patterns. When two or more patterns occurred simultaneously the pattern with the highest number was actually registered in the protocol. The first code, 01, was used when a monkey was not observable.

02: sitting upright; the monkey sits with his feet and possibly his hands resting on the ground; his head is upright and he is more or less passively monitoring the environment.

03: sitting hunched; the head is bent down forwards and the arms and hands are often held between the legs.

04: standing on all four legs

05: standing upright; on hindlegs; includes leaning against some part of the cage.

06: lying on side

07: lying on back

08: walking; on two, three or four legs, with regular steps.

09: climbing; moving along a vertical or tilted plane.

10: brachiating; moving by the hands alone while hanging under a horizontal or tilted plane.

11: shaking head; the monkey sits or stands and shakes his head with a vigorous rotating movement.

12: shaking body; the monkey sits or stands and shakes his whole body; the movement starts with the head and courses backwards.

13: scratching quickly; quick, rhythmic movement of the foreleg or hindleg; reflex-activity.

14: scratching slowly; with one hand; both patterns (13 and 14) are usually performed without visual control.

15: grooming himself, including cleaning of wounds; usually one hand is used while the other hand explores the area thus exposed; the monkey looks at the area of grooming.

16: licking himself; parts of the body, especially when wounded.

17: rubbing nose; with one hand

18: rubbing eyes; with the back of the hand

19: stretching; the monkey is standing, sitting or lying and

stretches his whole body or just his legs.

20: yawning; usually when sitting

21: anogenital inspection; the anogenital area is touched with the fingers and often the monkey looks at, smells, or licks his hand afterwards.

22: urination

23: defaecation

24: looking; the monkey is looking at objects at a distance or held in his hand; includes looking into small holes or under objects.

25: orienting; the head is raised and directed at the source of a sound or at a visual stimulus.

26: going towards; locomotion in the direction of an object

27: going away from

28: alarm reaction; interruption of all ongoing activity; usually followed by a rush towards shelves in the back of the cage.

29: sniffing at; by bringing the nose close to an object or by picking up an object and holding it near the nose.

30: manipulating objects held in the hand or parts of the cage

31: licking objects (either held in the hand or fixed in the cage); sometimes objects are put in the mouth.

32: biting in an object

33: picking up an object

34: rubbing objects, especially food pellets, between hands or between hand and substratum.

35: eating and chewing; not only food but also pieces of wood

36: drinking, either by sucking at the water tap or by licking the hands and wrists after they have been made wet.

37: slapping the ground; with one or both hands

38: bouncing; grasping the floor or the wall of the cage with both hands and feet and vigorously shaking it.

39: staring at; eyes widely open and fixating the partner

40: facing away or avoiding looking at another monkey

41: flattening the ears; retracting the ears backwards and holding them against the head

42: scalp retraction; retracting the skin of the forehead

43: lifting the eyebrows

44: bared teeth grin; retracting the upper and often the lower lips as well; the mouth stays closed.
45: open mouth; the lips remain covering the teeth
46: open mouth grin; the teeth bared with open mouth
47: puckering the lips; protruding the lips while the mouth remains closed
48: lip-smacking; rapidly opening and closing the mouth; sometimes with protruded lips.
49: tongue smacking; lip-smacking while the tongue moves rapidly backwards and forwards.
50: head bob; thrusting the head forward in the direction of a partner
51: shoulder bob; more intense than head bob
52: lunge; a quick movement of the forelegs only, in the direction of another monkey.
53: shrinking; the monkey sits or stands and moves his upper body quickly backward
54: crouching; flexing the knees and the elbows and pressing the body against the floor
55: presenting sexually; standing with the hindquarters directed at another monkey; the forelegs may be flexed; sometimes the head is turned backward to look at the other monkey.
56: presenting for grooming; lying, sitting or standing near another monkey and adopting postures which elicit or facilitate grooming by others; in particular, exposing the chest and the neck or the anogenital area (as in sexual presenting).
57: moaning; soft, humming-like noise; the mouth is slightly open
58: grunt; vocalization with a somewhat retracted scalp and slightly open mouth; it sounds like "chrroh" or "chrreuh" and is often repeated by other monkeys.
59: threatening grunt; vigorous sound "rrr" emitted with the head thrown backward and the chin pointed at another monkey.
60: warning grunt; a forceful and repeated sound like "rho"
61: scolding; a short sound like "kah", emitted rhythmically and often repeated by others
62: screaming; a high-pitched sound like "krii", often occurring together with an open-mouth grin.

63: shrieking; as screaming, but of a much longer duration
64: cackling; rhythmical vocalization of females, in particular during or after copulation
65: approaching; any slow locomotion (walking, climbing, brachiating) towards another monkey that remains still
66: running at; fast approach
67: going away from; any slow locomotion away from another monkey
68: running away from; fast locomotion
69: chasing after; usually fast locomotion towards a monkey that
70: is fleeing away from its follower
71: joining; slow locomotion towards a partner who is also moving
72: pointing; approaching another monkey (with a threatening expression) but staying a short distance apart while emitting threatening grunts and looking intermittently in the direction of other animals.
73: walking out; specific behaviour of female monkeys, immediately after copulating; it consists of running or jumping away over a short distance after the male has dismounted; often accompanied by cackling.
74: touching; putting the hand on the body of a conspecific and holding it there for a while
75: grooming; other monkeys; see 15 for details; allogrooming often occurs together with lip-smacking.
76: being groomed; accepting grooming activity from another monkey
77: grooming directions; correlative of 76: the grooming monkey determines the posture of the partner by direct manipulation of his body.
78: being directed; adopting postures passively, i.e. directed by the grooming monkey (correlative of 77)
79: inspection; moving head towards another monkey's body and sniffing or tasting
80: mouth-mouth; moving mouth against that of a partner, often reciprocally
81: anogenital checking; particular form of inspection, directed at the anogenital area of the partner
82: mounting; a monkey clasps the calves of its partner's legs and grasps its loins, sometimes kneading the fur; usual

male posture in heterosexual copulation, but occurs also between males and between females.

83: copulating; rhythmical movements of the pelvis while mounted

84: ejaculation; interruption the pelvic thrusts; tremor observable in the muscles of the hindlegs; often accompanied by a facial expression resembling a grin.

85: fetching and grasping (and holding)

86: pulling and tugging

87: blocking; defending the body against physical assault by raising the arms

88: pushing away

89: striking at and hitting the body of another monkey

90: striking at but "deliberately" missing the other monkey by changing the direction of the hand movement just before hitting.

91: biting; during a fight

92: wrestling; usually reciprocal: the monkeys hold each other's bodies or arms and lightly bite each other or hold their mouths slightly open.

94: tail contact; a monkey sits near another monkey and lets his tail rest on the tail of the other

95: hiding; after fleeing the monkey sits opposite another monkey, alternately looking at him and grinning at his former opponent

This list of behavioural patterns has been mainly based on a provisional ethogram compiled by Timmermans and his co-workers in 1974. It has been employed in most of the experimental work reported on in the following chapters. With regard to the type of definition used, it is clear that most of the behaviour patterns are identified by one essential element. Further details on the behaviour of Java-monkeys can be found in Angst's monograph (1974) and Welling's survey (1977), which also contains many comments on comparative nomenclature. The extensive descriptions of the behaviour of stumptail monkeys by Bertrand (1969) and Chevalier-Skolnikoff (1974) are also useful for understanding the behaviour of Java-monkeys.

During the period that the ethogram described in the preceding section was used, it gradually became clear that several serious problems are associated with its design, in fact with the use and design of any ethogram. They will be discussed briefly with special reference to the case in hand, the description of Java-monkey behaviour.

Purpose of an ethogram

The purpose to be served by the ethogram should be fully clarified. Observation of behaviour can be used to detect effects caused by various experimental treatments of the behaving animal, ranging from changing the conditions of development to direct interference with the physiology of the organism. In this case, behaviour is mainly an indicator variable, something by which certain effects become manifest. However, interest can also be focused on the observed behaviour itself, in questions concerning the structure and organization of behaviour. It should be evident that any theory on the way behaviour is programmed and executed depends heavily on the way behaviour is described and recorded. It can even be argued that any description of behaviour is in fact a theory of the behaving organism ("description" can be considered as the weakest or least constrained type of "measurement"). This point will be elaborated below.

Although there appears to be a logical distinction between both objectives in describing behaviour, it is not quite clear whether it should have practical consequences. Perhaps the distinction does not justify a difference in the way behaviour is described. After all, it could be maintained that any phenomenon revealed by behaviour as an indicator variable can only make sense if it can be interpreted in terms of the intrinsic structure of behaviour. However this may be, the distinction is relevant, for the aims of our work were two-fold: to investigate the way ongoing behaviour of Java-monkeys is organized in a social situation, and to specify the function of the caudate nucleus in the organization of behaviour. In view of our first aim, the ethogram to be used should be appropriate or valid with respect to the structure of

behaviour. "Validity" in this context means that the structure of the description of ongoing behaviour is isomorphic with the structure of the behaviour itself, that is, the ethogram must provide an appropriate space for representing or mapping the observed behaviours and their relationships. To ensure this, the implicit structure of any ethogram must be made explicit or purposely imparted to it.

Formal requirements: the structure of an ethogram

The problems associated with the logic in constructing an ethogram are particularly relevant when the observation of behaviour is to provide knowledge on the organization of behaviour. The ethogram, defined as a set of behaviour patterns, must meet some formal requirements. Above all, the set must have a structure (provided by specifying a topology or a grammar for the set). The proposed structure can at the same time be considered as a theory of the animal as a behaving system. This requirement has been recognized, more or less implicitly, by several authors dealing with the topic of the structure of behaviour. In general, two strategies have been used to define a structure for the set of behavioural states. The first strategy may be identified as empirical or *a posteriori*, and is closely linked with the area of psychological research called "attribution theory". The "stream of behaviour" and the way it is perceived as structured in "behaviour units" are studied primarily from the viewpoint of the observer (Barker, 1963; Dickman, 1963; Wright, 1967; Newtson, 1976; Bregman, 1977). A concrete example of structuring an ethogram is provided by Maxim (1976) working with rhesus monkeys. The second strategy is more rationalistic or *a priori*. It has been developed mainly in the context of describing and measuring animal behaviour. The behaving organism is viewed as a system with certain properties and the structure of this system is described in such a way that the observed behaviour reflects these properties (Russel et al., 1954; Kochen and Levy, 1956; Pike, 1957; Delgado and Delgado, 1962). One particular formal model for a behaving system would be a finite state automaton; such a model appears to be implicitly assumed by Delgado and by Kochen. The relationship between the

description of ongoing behaviour and a theory of the organization of behaviour was the starting point for Westman (1977). This author considers the "descriptive paradigms" currently used in ethology as inadequate, simply because they convey the wrong picture of the way behaviour is organized. He then develops an approach based on the theory of formal languages and automata.

However, the structure imposed on the ethogram need not be as specific as that associated with automata. Much less constrained formalizations are possible (Toda and Shuford, 1965; Roosen-Runge, 1966). Nevertheless, a minimum number of formal requirements must be met by any collection of behaviour patterns in order to qualify as a workable ethogram (see also Slater, 1978). It must be 1) complete and unambiguous, 2) homogeneous and 3) consistent. The first requirement is intuitively clear; the observer must be able to identify with certainty the particular state of the animal at any time. Certain mathematical methods are applicable to this problem (Fagen, 1977, 1978b). Homogeneity can be defined as the property that all elements in the ethogram are comparable along the same dimension. Behavioural patterns can differ in many aspects (Chamove, 1974): intensity of the physical exercise (e.g. touching vs embracing vs hitting), gradation along the dimension molecular-molar or in the number of effectors involved, the possibility of an arbitrary duration (e.g. yawning vs walking vs grooming). The identification and selection of relevant dimensions is again a matter of having an implicit or explicit model. Consistency is the most essential property when the structure of behaviour is under study. For our purpose it can be defined as homogeneity with respect to the relationships between the elements in the ethogram, in particular with respect to the way any given behaviour pattern imposes constraints on preceding, simultaneous or subsequent patterns in the subject itself or in its partners. That is, for each behaviour in the ethogram it must be clear that its occurrence has no a priori implications for the occurrence of other behaviour patterns. This requirement may be weakened to the following: all behaviours in the ethogram must be equal in the kind and degree of constraint they impose on each other. The requirement of homogeneity ensures that observed relations between

behaviours, for instance correlations, can be given equal weight in inferring some structural property of the organization of behaviour. (The concept of homogeneity is related to the concept of degrees of freedom. See the section on Statistical Procedures of chapter 8.)

When these criteria are applied to the currently available descriptions of Java-monkey behaviour, homogeneity and consistency are found to be only partially present. This will be illustrated by the way passivity and simultaneity are handled. In our ethogram we defined patterns called "being groomed" and "being directed by a grooming monkey". The inclusion of patterns of this kind can be intuitively justified as follows. The observer of behaviour is interested in any state of the animal and attempts to identify states that are different from each other. Clearly, sitting alone is different from sitting in the immediate vicinity (within arm's reach) of other monkeys. Sitting near another monkey also differs from sitting near a monkey and being groomed by it. One might argue that the states "sitting near" and "being groomed" could be considered as separate activity patterns, on an equal footing with other patterns, such as "grooming" or "eating". They are behaviours of a subject or actor, because a monkey can initiate and terminate these states by itself: it can approach another monkey and leave it, it can invite for grooming and refuse being groomed by moving away. We have therefore a particular kind of activity, namely passive activity, which represents a state of the monkey that is similar to normal activity, in that the monkey has some control over the occurrence of the state. (Purely passive states do not have this property: "being looked at" is not normally under control of the subject that is being looked at.) Although passive activities therefore appear to be acceptable, they do create problems: their definition presupposes other, active behaviour patterns in the ethogram (allowing the onset and termination of the passive activity). In fact, the empirical context of such states is also constrained: not every activity can preceed or follow passive activities. This creates lack of homogeneity in the ethogram: some behaviours are restricted to particular sequential contexts, others are not, or at least not to the same

degree. This problem is not limited to passive activities. The pattern "copulating" for instance presupposes "mounting", but "mounting" need not be followed by "copulating". In this case the patterns "mounting" and "copulating" are not completely independent.

The problem of simultaneous behaviours

Several pragmatic solutions are currently used for dealing with simultaneously occurring behaviour patterns: 1) combining two separate patterns in the definition of a new pattern or isolating an element of a pattern and defining it as a pattern on its own; 2) using priority rules to select one of the simultaneous behaviours as the most relevant one; 3) coding behavioural states as a vector variable. Each of these solutions affects the consistency of the ethogram.

Treating a combination of two patterns as a new pattern in its own right has been done repeatedly. For instance, Angst (1974) defines the behavioural element "Imponierendes Schwanzaufrichten" as "Initiatives Aufrichten des Schwanzes, oft mit Vornüberbiegen" (des Schwanzes) (p. 87). This element, together with the optional element "Fellsträuben (p. 23), constitutes at the same time the behaviour pattern "Imponierendes Schwanzaufrichten". Together with other elements ("Fixieren", "Vorstrecken des Kopfes", and "Ohrenanlegen") the element "Imponierendes Schwanzaufrichten" constitutes the behaviour pattern "Imponierendes Anvisieren" (p. 26; at the same time a pattern also exists which is defined only by "Fixieren", "Vorstrecken des Kopfes", and "Ohrenanlegen", p. 52). Similarly, De Waal et al. (1976) use the patterns "staring" and "open-mouth"; the latter consists of staring with an open mouth (pp. 251-262). This solution was in some cases used in our ethogram too; "open-mouth grin" was for instance defined as "open-mouth" together with "bared teeth"; the latter elements also occur separately. There is nothing unacceptable with this solution except that it is often used rather inconsistently. When it happens that two behaviour patterns which can occur in isolation can also occur together, the combination always can be treated as a new pattern. This is usually done on the basis of

observation. However, many patterns could "in theory" occur together, since we can give no special reasons why some patterns are not observed together. To give an extreme example, the patterns "sitting hunched" and "bared teeth grin" are not incompatible, but they are not to be expected to occur together. One might propose as an a priori explanation the fact that "bared teeth grin" is a communicative pattern, intended to affect the behaviour of other monkeys: when the animal is bending its head down, the "bared teeth grin" would scarcely be effective. This explanation however presupposes a knowledge of the function of the pattern, which is often supposed to result from an analysis of observed behaviour. (See for instance Altmann's attempt to bypass a priori assumptions in the definition of communication; Altmann, 1965.) It is difficult to establish a priori for each theoretically possible combination of patterns that its actual existence can be disregarded. When observation determines such decisions, the size of ethogram becomes a function of the total observation time (Fagen, 1977). Conversely, non-occurrence of a particular combination of patterns can be due just as much to sampling insufficiency as to intrinsic constraints in the structure of behaviour. The acceptance therefore of combinations of separate behaviour patterns actually observed and the omission of combinations which for some reason are not expected, distort the homogeneity and consistency of the ethogram, unless a similar reason applies to all other behaviours.

What has been said on the combination of patterns into additional ones also applies to the isolation of elements from patterns and their treatment as separate patterns. For instance, the patterns "Stummes Hetzen" (Angst, 1974, p. 20) is specified by the following elements: "Fellsträuben", "Fixieren", "Vorstrecken des Kopfes", "Brauenheben", "Lidsenken", "Ohrenanlegen", "Blick nach Unterstützung", "Präsentieren" and "Präsentierendes Schwanzaufrichten". The last three elements are optional: they occur, sometimes or often, together with the other elements. The element "Blick nach Unterstützung" is in particular often present in the pattern. The only behaviour pattern however in which this element occurs is "Stummes Hetzen", and this element would formally be

redundant. But from further descriptions by Angst it can be inferred that this element is quite essential for the patterns "Stummes Hetzen". Similarly, the behaviour patterns "Hetzen mit Grunzen" (Angst, 1974, p. 20-21) is defined by the same elements as "Stummes Hetzen" and, additionally, "Drohgrunzen" or "Doppelgrunzen"; optionally, "Straffen der Gliedmaszen" can be added by the animal. This latter element is mentioned only in the pattern "Hetzen mit Grunzen".

These examples illustrate two kinds of inconsistency. Firstly, when one pattern is defined by the same elements as another (with some additional elements of its own), it should be made clear whether the optional elements of the first pattern carry over to the second pattern. Secondly, when ongoing behaviour is recorded in terms of the patterns cited, information on the occurrence of the optional elements is lost; although they were apparently considered important enough to deserve being mentioned separately. Perhaps this is the reason why De Waal et al. (1976) identify them as patterns in their own right: "showlooking" corresponds to "Blick nach Unterstützung" and "stiff approach" to "Straffen der Gliedmaszen". Both elements can occur independently or in combination with other elements. In the latter case, they constitute the patterns "pointing" (equivalent to "Stummes Hetzen") and "serial grunt" ("Hetzen mit Grunzen"). The practice of isolating elements from a pattern and treating them as separate patterns threatens the homogeneity and consistency of the ethogram in much the same way as the opposite proces (combining patterns into additional ones). Elements can of course be identified perceptually and defined on their own; this fact is indeed the basis for the possibility of describing behaviour at all. But in practice, elements always occur together with other elements. The decision to regard these other elements as irrelevant background variation is often based on intuitive considerations. Again, there is nothing wrong with this, as long as such considerations remain the same for all elements and are applied with equal weight. Any pragmatic ad hoc solution in the definition of behaviour patterns is equivalent to an ad hoc hypothesis.

Another solution for dealing with simultaneous behaviours is

the use of "priority rules", as proposed for our own ethogram. The problem remains, however: these rules are often established quite intuitively and represent additional hypotheses on the structure of behaviour.

It would appear that the best way to deal with simultaneity is to use a vector ethogram, not only for defining behaviour patterns but also for recording ongoing behaviour; behaviour can be registered simply by writing down the vector of separate components making up a behaviour pattern. No decision has to be made on which elements are important and which irrelevant; the ethogram would not be a collection of patterns lacking homogeneity some mutually exclusive with others partly overlapping and still others different but combineable. There are however some drawbacks. The multidimensional state space for behaviour would soon become too large for convenient handling; a vector registration of behaviour would be rather demanding as regards the recording of ongoing activity (see for instance Condon and Ogston, 1967; also Golani, 1973) and the effective analysis of the data. A more theoretical difficulty arises with the interpretation of a multidimensional behavioural space, as illustrated by the following example: Shirek-Ellefson (1967) identifies three distinct states for each of seven components determining facial expression. For instance: the head can be held in the normal position, raised, or lowered; the mouth can be closed, open or in motion (opening and closing); the ears can be in the normal position, brought forward or retracted etc. Theoretically, such a scheme allows for $3^7 = 2187$ different facial expressions. When complete behaviour patterns are specified in this way, the number of possible patterns is astronomical. The considerable theoretical freedom in composing behaviour patterns is not matched by the quite small number of observed patterns: Shirek-Ellefson discusses only nine different facial expressions! Perhaps the underlying model of the vector approach, the idea that an organism can be broken down by independently operating subsystems, is not appropriate. It is quite conceivable that monkeys have been evolving in such a way that particular values of one component constrain values of other components. In that case the theoretical state space generated by

the components of the system is a somewhat irrelevant universe of discourse; a better model for the generation of behaviour patterns would be a set of syntactical rules. The following rather ludicrous analogy may serve to illustrate the point: all sentences of 200 characters or less can be generated by a vector of 200 components, each component having a range of some 35 values (including markers). It is obvious that this formal structure for representing sentences does not represent the way sentences are constructed in practice. The foregoing discussion once again stresses the need for an appropriate choice of behaviour elements and thus for a theory of the formal organization of behaviour.

Inter-observer reliability

A final set of problems associated with ethograms in general is that of empirical content and reliability of definitions. Apart from the logical structure of the description, each item has to be defined in such a way that it can be easily recognized by others. In practice, most of the elements and patterns of behaviour of Java-monkeys offer no special difficulties: they are recognized quite quickly by the observer; it is also relatively easy to convey the definition of the patterns to other observers, by what is called "ostensive definition", i.e. merely by pointing or by any other non-verbal means. Difficulties arise when the scope of a pattern has to be described verbally. The situation may be illustrated by the following analogy. It is easy to define "red" by pointing at all kinds of red things, while it is surprisingly difficult to define "red" verbally, for instance by using other words that have meanings of their own. Such definitions can be so general that they describe an abstract concept instead of a concrete property (e.g. colour, when it is said that "red is light of a particular wavelength"); they do not therefore differentiate between different instances of the same concept, or they are so concrete as to require specific instruments to identify the wavelength in question. Problems of this kind arise when the vocalizations of Java-monkeys have to be defined. It is not difficult to identify particular sounds by means of sound spectra; Goustard (1963) provided in this way a detailed description of vocal com-

munication patterns in Java-monkeys. Angst, however, did not record sound spectra and described the vocal patterns he identified by means of phonetic approximations and by additional information concerning the behavioural and social context of the sounds. Real difficulties arise when attempts are made to establish a correspondence between Goustard's and Angst's descriptions (see for instance Angst, 1974, pp. 72-73). The identification and labelling of vocalization have been the subject of several discussions in which Timmermans and Van Hooff and their co-workers participated. Some issues were quickly settled by "ostensive definition": merely by playing back the vocalizations recorded on magnetic tape. The descriptions in our list are to be regarded as mnemonics rather than as verbal equivalents of the physical sounds (the same caveat applies to many other descriptions in the list).

The adequacy of definitions in covering the empirical content of single behaviour patterns is only a first-level problem. In addition, it is mandatory to ensure sufficient coverage of the stream of behaviour as it proceeds over time. This is particularly relevant when sequential relationships between behavioural states, or the dynamical structure, are under study. Evaluations of particular sampling strategies are available (Fienberg, 1972; Altmann and Altmann, 1977; Chow, 1977; Leger, 1977; Simpson and Simpson, 1977) as well as general reviews of the methodology involved (Altmann, 1974; Dunbar, 1976; Shapiro and Altham, 1978).

To summarize, several problems are associated with the description of behaviour: firstly, the issue of the instrumental value of an ethogram; secondly, problems of the logic in constructing ethograms; thirdly, the problem of simultaneously occurring behaviours; and, finally, practical matters concerning the empirical content of the descriptions. The second and third problem have been discussed at some length, since various intuitive ways of defining patterns of behaviour affect the homogeneity and consistency of the ethogram. In particular, the way in which simultaneously occurring behavioural elements are treated was singled out as a potential threat to consistency. Explicit criteria applied in a rigorous way are needed to establish a set of behavioural patterns that can serve as an appropriate space for mapping ongoing behav-

iour. Only when the ethogram has a sufficiently rich and consistent formal structure of its own, can it be used to represent empirical behaviour and at the same time provide additional understanding of the intrinsic structure of behaviour. In short: a good ethogram is a good model of behaviour; the converse need not be the case for an ethogram that is not a good model of behaviour can still give a good description of behaviour. The currently available ethograms are admirably rich in empirical content and provide a great deal of information on many aspects of individual and social behaviour. However, the task of constructing a paradigm for describing natural behaviour to meet certain formal criteria is a task for the future.

PERSPECTIVE: A SYNTACTICAL PARADIGM FOR DESCRIBING BEHAVIOUR

To conclude this discussion some reflections are offered on the nature of behaviour and some suggestions for an ethogram for the analysis of ongoing behaviour. It is first of all necessary to shift attention from the morphology of the behaviour pattern to the function of behavioural activity. Morphological variation converges in the purpose of behaviour, i.e. on what is accomplished by behaviour (the consequences of behaviour in Hinde's terminology (1970)). An animal is continuously interacting with its environment and behaviour is only a means to maximize the organism's profit from environmental resources such as energy and matter.

The behaviour of an animal is not exempt from the general law of evolution: "adapt"! Behaviour evolves as a means of adapting to changing external conditions, either by passive reaction or by active manipulation. Consequently, behaviour is to be described in terms of the relation between the animal and its environment. Behaviour can be defined and therefore accordingly measured as the difference between the state of the world (including the animal) at time $t+\Delta$ and at time t. Any measurable change in the environment caused by the animal or the choice of a change in the animal-environment relationships is behaviour. This definition is the opposite of the stimulus-response view of behaviour as

any change in the animal caused by the environment; the definition can still considered to be behaviouristic (Powers, 1978; cf. also Tembrock, 1973).

The structure of ongoing behaviour is the result of the interaction between constraints due to the structure of the environment and constraints due to the design of the organism. Unitary items of behaviour are established by unitary interaction with the environment. An "piece of behaviour" can be isolated by identifying its environmental correlate: its object and, accordingly, its purpose. In concrete terms: a behaviour pattern is an activity or just an act, identified by its object. "Objects" can be practically anything, from inanimate things to conspecific animals, in monkeys perhaps even simple abstract entities (for instance, the distance to be maintained between animals). Further differentiation between types of acts can be accomplished by breaking down a pattern into a minimum number of elements: when an activity pattern, directed towards the same object, can vary in composition, as many elemental acts are defined as are necessary to reconstruct each of the patterns. For instance, the various patterns of "sexual presenting" in a female monkey can be broken down into the following separate acts: "adopting an oriented posture" (defining element), and "looking in the direction of the partner" (optional element). The breakdown is valid because 1) both of the acts can occur separately and 2) both of the acts can occur in other contexts. I should like to stress these criteria, because when it is realized that the same acts are indeed executed in different behaviour patterns, an analysis of ongoing behaviour can concentrate on how elemental acts are used as sub-routines in composing activity patterns. The act mentioned above, adopting an oriented posture, can also be carried out when an animal invites grooming. Instead of listing two "different" patterns, "sexual presenting" and "inviting grooming", we could better list a single act, "adopting an oriented posture"; the variability or flexibility in behaviour rests in the fact that the very same act can serve different objectives. (The situation may be clarified by an analogy: "putting down" is the same act, whether it is done with "a book" or with "a glass of water", and whether things are put down be-

cause they are too heavy or because the hand is needed for another purpose).

When these considerations are applied to the problem of constructing an ethogram, we arrive at the following formal scheme for describing behaviour. A monkey can be interacting with one or more objects in the immediate environment and it can engage in one or more elementary activities with respect to each object. Merely brief observations of monkeys reveal that sometimes they do nothing in particular, that is to say they are not engaged in object-directed activity. A monkey must nevertheless be doing something, that is a monkey somehow must be somewhere: let us say that a monkey that is apparently not busy with a particular object, is in a basic state. It can easily be observed that the condition of not being engaged in object-directed activities can be differentiated by mutually exclusive states (e.g. lying, sitting, standing). Finally, it can be observed that basic states are also involved when the monkey performs object-directed activities. The resulting paradigm for describing behaviour can be represented by the following syntactical formula:

$$S : B \{A(..) O\} \{..\}$$

The behaviour at any time of a subject S can be described as consisting of one basic state B, to which one or more act-object clauses can be added; each act-object clause consists of one or more acts A directed at an object O. Basic states are defined as mutually exclusive patterns of locomotion or posture; they are necessary conditions for any activity or interaction with the environment. The formula generates a variety of patterns. For instance, a monkey is simply lying down, (S : B); it is sitting and grooming a conspecific animal, (S : B A O); it is standing and presenting to one animal and at the same time threatening another (S : A O A O); it is grooming another monkey and lip-smacking at him (S : A A O) etc. The proposed scheme is quite close to a common natural-language description. It is possible that natural-language syntax has evolved in order to match the natural organization of behaviour (cf. Schank, 1973; Schank and Abelson, 1977). This approach of describing behaviour in the form of simple

sentences is much more flexible than the earlier method of representing the stream of ongoing behaviour by means of mutually exclusive states. In the following chapter some details are given on how it can be implemented in a procedure for protocolling behaviour.

CHAPTER 3

RECORDING AND PROTOCOLLING BEHAVIOUR

THE RECORDING PHASE

Ongoing behaviour is too complex to be studied by instantaneous visual and auditory monitoring alone. The stream of behaviour must be preserved in the form of a record and/or protocol. Many kinds of protocols have been used, from simple notes written down during actual observation to laborious protocols based on film- or video-records of the observed behaviour. The methodology and techniques of protocolling have become quite sophisticated during the last decade; general reviews are provided by Hutt and Hutt (1970) and by Vowles (1976).

This chapter describes the equipment for recording and protocolling the social behaviour of Java monkeys that was used in the experiments to be reported on in later chapters (6, 7, 10, 11 and 12). The general arrangements were developed by Cools of the Laboratory of Pharmacology and by technicians of the Faculty of Sciences, all of the University of Nijmegen. During the past few years a number of modifications and improvements have been added. The equipment will be described as it is presently operating. Several authors have described more or less similar systems (Stephenson et al., 1975; Taylor et al., 1975).

The general arrangement of the system's components for observing and recording is illustrated in Fig. 3.1. The monkeys to be studied live permanently in a special cage inside a Faraday cabin. Their behaviour can be monitored and recorded by means of a video-recorder and two cameras. One camera is fixed and provides a wide-angle survey of the cage, while the other is equipped with a remotely controlled pan-tilt mechanism and zoom

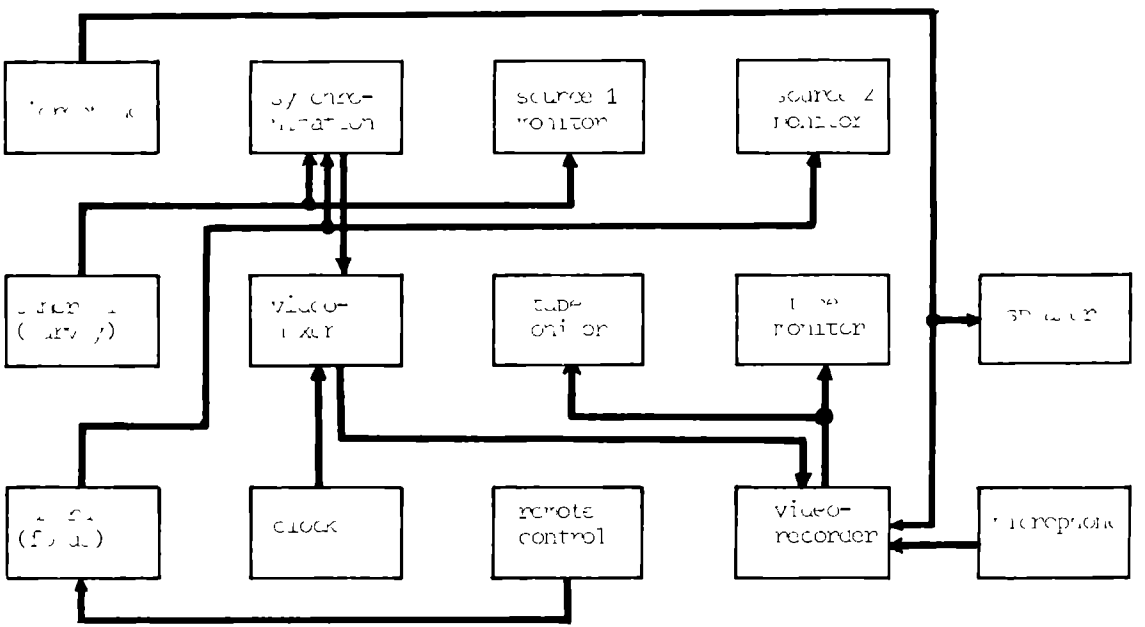


Fig. 3.1
System for observing and recording behaviour

lens, and can be focused on any particular place in the cage. The signals from both cameras are synchronised, combined with signals from a digital clock and recorded on videotape. The time-signals are recorded on the tape in two different formats: as the usual display-numerals for immediate reading by the observer, and as binary-coded signals for an interface connected to a minicomputer. Four TV-monitors are in use: two for monitoring the source-signals (i.e. the output of the two cameras) and two for monitoring the tape-signals (i.e. the output of the video-recorder, consisting of the source-signals together with the time codes).

During an observation session the signals from the focus camera are usually recorded. Sometimes however the overall group configuration, monitored by the survey-camera, is important. It is possible to record the signals from the survey-camera simply by operating a switch. In special cases information on both the monkey in focus and on other monkeys elsewhere in the cage may be relevant: both signals can in such a case be simultaneously recorded on the tape. (Half of the lines defining the usual video-image are allocated to each of the sources; therefore the advantage of obtaining information from two sources must be weighed against the loss of precision.)

The sounds emitted by the monkeys are monitored with a speaker in the registration room and can be recorded together with the video-signals. Lastly, the observer can record on-the-spot comments arising during an observation session by means of a microphone, sharing access to the audiochannel of the video-recorder with the microphone from the monkey cage.

THE TRANSCRIPTION PHASE

The recording of behaviour on videotape means that it is permanently available for further processing. The format of the data on the videotape is however rather difficult to manage: the only way to evaluate the data is to reduce and recode its content. Two approaches are possible. Firstly, the kind of information that is considered relevant to the problem under study can be

specified a priori and the corresponding data can be extracted from the tape without much trouble. An example might be the number of animals involved in a particular kind of interaction, or the frequency or duration of a particular behaviour pattern. This type of information can usually be obtained by playing back the tape just once and accumulating the desired information on a simple device. The disadvantage of this approach is that when questions arise that cannot be answered by the information retained in the protocol, the videotape has to be screened once more. The second approach is intended to avoid this situation, but is at the same time more laborious. It consists of making a verbal transcription of the content of the tape in such a way that a broad range of relevant data is covered which can be easily retrieved from the protocol. When the structure of ongoing behaviour is to be studied, this latter approach is almost always to be preferred. The task then is to design a protocol format that meets the following requirements. It must be able to retain as much information as possible without too much preprocessing, and it must not be excessively time-consuming. Moreover, it must be so general and flexible that it can be easily adapted and extended as the research proceeds.

The traditional steps in handling observational data are the following. The observed phenomena (1) are recorded on some medium, (2) e.g. a note book or a videotape. The relevant aspects are selected and coded on a protocol form or a check-sheet (3). The data are subsequently recoded in a format appropriate for computational procedures (4) e.g. punch cards. In the next step, some data reduction provides tables, graphs and summary statistics (5); further data analysis finally results in information that corresponds to the parameters of some hypothesis or theoretical model. This process can be simplified considerably when a microprocessor is used; such an instrument equipped with the appropriate peripherals offers the possibility of programmable check-sheets and interactive protocolling. Such an arrangement was used in our experiments. The system adopted, which was designed around a microprocessor (PDP 11/03 LSI) with 28 K words memory (INTEL), a videoterminal (Tracor 100) and a floppy disk

(Plessey), is illustrated by Fig. 3.2.

As soon as the observer stops the video-recorder, the digital time signals on the tape are decoded and inserted in the appropriate location in a pre-programmed protocol form displayed on the video-terminal. The observer proceeds by comparing what he sees on the TV-monitor with the definitions of the ethogram and enters alpha-numerical codes for the patterns identified in the protocol form by means of the video-terminal's keyboard. The codes are immediately checked for their lexical and syntactical validity by a program in the microprocessor that uses information stored on the ethogram (vocabularies and rules for sequences of codes). In the event of an error, a message is displayed on the screen of the video-terminal and appropriate measures can be taken by the observer. When the codes entered are correct, they are filed on the floppy disk. On occasions when only some aspects of the behaviour are different from the situation coded, only the changed codes have to be entered in the protocol; the codes still in effect are inserted automatically by the processor. When the videotape has been completely processed in this way, some elementary data on the protocolled behaviour is immediately available: in particular, tables of the frequency and duration of each behaviour pattern occurring in the protocol can be produced.

In the procedure described, therefore, the traditional steps of manual processing (3) and (4) are combined into one transcription phase; during the transcription phase the processor accumulates summary statistics on the protocol, and in this way step (5) is also immediately executed. The central role in this procedure is played by the microprocessor, which has five functions in the protocolling phase: to provide a programmable protocol form, to check the codes entering the protocol, to insert the time code directly from the videotape, to insert codes that remain on certain occasions unchanged and to provide summary statistics at the end of the protocolling session. The first two functions will be described in greater detail.

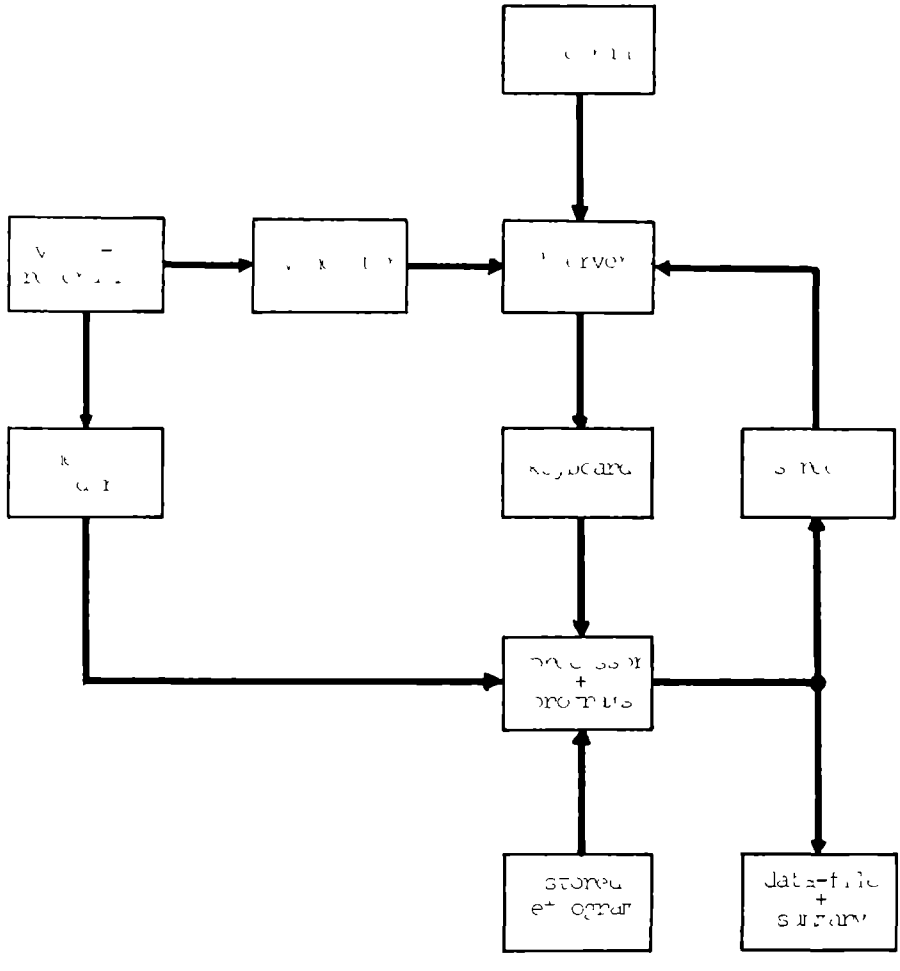


Fig. 3.2

System for interactive protocolling of behaviour recorded on videotape

In the design of the protocol the Format- and Edit-facilities of the Tracor video-terminal were used, partly under the control of a program in the processor. The screen of the video-terminal can accommodate 24 lines of 80 characters. We used two types of format for this matrix; the first provided a fixed format protocol and the second one a free format protocol. In the fixed format protocol the 80 positions per line were allocated both to the time code (7 digits followed by 3 blanks) and the codes for the behaviour of one or more subjects. The distribution of the positions of the codes can be assigned at the beginning of each protocolling session either by specifying the necessary positions one by one or by recalling a pre-programmed format from the processor. In most of the experiments to be reported upon we described the behaviour of three monkeys by numerical codes for behaviour, location, and orientation. One line of the protocol contained therefore both a time code and codes for the simultaneously occurring behaviour of several monkeys. A new line was entered by the observer as soon as one of the monkeys changed its behaviour in any respect, while the codes that were not changed were inserted by the processor. The resulting protocol had therefore the same lay-out as a data matrix consisting of successive series (rows) of individual state vectors (columns), which was convenient for further processing.

The free format protocol was designed to describe the behaviour of monkeys in groups of six to eight. In this type of protocol literal codes were used (two to four letters per code) and the codes were entered according to a simple syntax. (This system was based on the principles outlined in the preceding chapter.) In the free format mode of protocolling one line is used to describe the current state of each animal. The first ten positions of the line are for the time code (7 digits and 3 blanks); a code for the subject itself and codes for its behaviour follow. Again only changes had to be keyed in; the rest was supplied by the processor's memory. In practice, this means that when the video-recorder is stopped, the relevant time code is displayed along with the names of the monkeys in the group. The cursor of the video-terminal then moves along the lines of the code loca-

tions until it is stopped by the observer. When the cursor is positioned at the beginning of a name the observer can a) skip the line for this subject; b) indicate that the preceding state codes for this subject are still applicable; or c) interrupt the cursor when it reaches a location were new codes have to be entered.

To complete this discussion of observational methodology, a short description will be given of the program used to check the codes entered in the protocol.

A PROGRAM FOR INTERACTIVE PROTOCOLLING

The following program, ENCODE, was written in Fortran IV for the PDP 11/03 operating under the RT-11 system. Fortran is not the most efficient language for this type of data processing, but it is the only suitable language available with the PDP microprocessor. The effort required to write the program in Assembler is not worthwhile, as the small amount of data and the low rates of data-acquisition do not impose any penalty in time or memory consumption.

Input

Successive blocks of one or more records (= lines) formed the input with as format for each record: time code (7I1, 3X), subject code and codes for the behaviour of the subject at that time (max. 13). The subject and behaviour codes are literal codes of 2 to 4 characters, separated by blanks (see below). The codes are listed in a reference lexicon (on Disk), and are entered according to the syntax outlined below.

Function

1. *Comparing the codes entered on the terminal with the codes in the reference lexicon (checking the lexical validity of the codes).* When a code has not been found in the lexicon, a message is sent to the terminal. The observer can respond either by correcting the entered code or by having the code added to the lexicon. In this way the lexicon can be extended or even newly

composed during the actual process of protocolling.
2. *Checking the validity of the syntax, from the presence of markers (see below).* The marker preceding a code defines the syntactical category of that code and when a code is not of an expected category, a message is displayed on the terminal. A particular syntactical category can be followed by a limited number of other categories; the markers are also checked for their admissibility.
3. *Converting the literal codes into 3-digit numerical codes.* The syntactical category of each code is now identified by the range of the interval of the numerical code (e.g. 001-010 are subject codes; 011-020 are codes of the same names but now functioning as objects).

Output

Output consists of blocks of records containing numerical codes describing the behaviour of one or more subjects at a given time. A new block is started when at least one subject changes its behaviour. The descriptions of other subjects appropriate at the same time are also added to that block. The format of output records is as follows: (7I1, 3X, 14I5).

Syntax

The following syntactical categories are employed:
- subject (Sb)
- basic states (BS)
- proximity (Pr)
- activity (Act)
- object (Ob)

A record containing the behavioural state description of a subject at a given time is composed according to the following syntax:

$$\text{Time Sb : BS } (\text{-Pr})^{\bigstar} \left[(\text{;Act})^{\bigstar} \begin{matrix} /\,\text{Ob} \\ \backslash\,\text{Ob} \end{matrix} \right]^{\bigstar} \left[(\text{\#Act})^{\bigstar} \begin{matrix} /\,\text{Ob} \\ \backslash\,\text{Ob} \end{matrix} \right]^{\bigstar} .$$

Square brackets indicate that the enclosed category is optional in the description while an asterisk indicates that the immediately preceding category (enclosed in brackets) may be repeated. Vertically ordered categories are mutually exclusive, meaning that one of the alternatives must be present. A behavioural state description consists of at least one basic state code. Basic states are mutually exclusive patterns of locomotion and posture, and one basic state is always present. As an option, basic states can be qualified by codes for proximity, indicating near which other individual the subject is located. Superimposed on the basic state, one or more object-directed activities may occur, or "act-object clauses". An act-object clause consists of one or more acts directed at one particular object or partner. Two types of activity are in use; identified by the preceding marker (either a semicolon '; ' or a number sign '#'). Activities of the first type are object-directed behavioural states that can have an arbitrary duration (i.e. their duration depends on the initiative of the interacting monkeys). Activities of the second kind are transient acts or "point events"; they cannot (normally) be prolonged at will. The reason for treating these types as separate syntactical categories is that for activities of the first kind both the onset and the termination must be entered in the protocol while for the point activities just one entry is needed. When the behavioural state of a subject has to be described as completely as possible, it is convenient to have an opportunity of adding "passive states", i.e. the behavioural activities which have the subject under study as object. The object category is therefore used in two different ways (indicated by the markers '/' or '\'). When the subject under study performs an act directed at another individual, the latter is coded as an object by a right-handed slash '/'; when the subject undergoes activities performed by others, the same codes for the activity are used, but the other individual is coded by a left-handed slash ('\'). It should be noted that the foregoing distinctions are not intrinsic to the function of the program. "ENCODE" provides the opportunity of using several syntactical categories and presupposes certain rules with respect to their

combination. The interpretation of the categories is however arbitrary and can be established by the user. The reason for using this syntax in the description of behaviour is not that it is the only one that is appropriate, but mainly that it creates the opportunity of handling different things (kinds of states), at the same time forcing the observer to do this consistently and correctly (by confronting him continuously with the syntactical rules).

Reference lexicon

For every syntactical category or subcategory a separate lexicon may be in use. Different lexica may contain identical codes (e.g. the names of the subjects may be found in lexicons for subject codes, lexicons for proximity-codes, lexicons for -objects and lexicons for -objects). It is also possible to have just one lexicon for all categories, using the same codes, but this reduces the opportunity for checking the syntactical validity of a protocol sentence. The maximum number of codes in all lexica together must not exceed 1000. The actual distribution of the codes of each category over these 1000 entries can be specified by the user; a specification by default is also available.

For the sake of completeness we mention the program package "PRIMATE", written by Humphreys (1974), and containing routines similar to the one provided by "ENCODE". However, since "PRIMATE" was designed for off-line data processing, it is, in general, much more complex than "ENCODE" and requires a 200 Kbytes core store on IBM 360/370 series computers.

CHAPTER 4

AN INFORMATION-STATISTICAL ANALYSIS-OF-VARIANCE MODEL FOR INTERACTION SEQUENCES

In a group of individuals living in a more or less unchanging environment, two factors are especially relevant for the occurrence of a behavioural state in any individual: the continuation of its own behavioural programmes and its reaction to the incidental behaviour manifested by others. When an individual changes his behavioural state or continues his behaviour after a change of behaviour in others, the selection of his next behaviour is determined by the set of possible behavioural acts; this selection is influenced by the preceding behaviour of the individual and that of his partners. Information-theoretical statistics can be used analogously to an analysis-of-variance, to measure the influence on the current behaviour of the reference subject of both his own preceding behaviour and that of others separately (McGill, 1954; Garner, 1962).

In ethology, research on animal communication took advantage of information theory as early as 1954 (Haldane and Spurway; see Hazlett and Bossert, 1965) and several models of social interaction have been proposed since (Altmann, 1965; Hazlett and Bossert, 1965; Hauske and Neuburger, 1968; Dingle, 1969; Mayer, 1971; Conant and Steinberg, 1973). The information-theoretical approach has been recently incorporated in the textbooks of Wilson (1975) and Hailman (1977). The current models in ethology are mainly designed to quantify the effects of communication, defining it operationally as the correlation between the behaviour sequences of several individuals ("interaction sequences"). In chapters 4 and 5 an analytical framework is developed for

measuring both inter-individual and intra-individual effects in interaction sequences. The relationship between both objectives will be discussed and the current information-statistical models of communication will be reformulated in analysis-of-variance terms and compared with our model. Mathematical models for analysing interaction sequences which are not based on informational statistics will not be considered (see Mayhew et al., 1971, and reviews by Slater, 1973; Metz, 1974 and Morgan et al., 1976).

STRUCTURE OF THE MODEL

Total individual variability

Let a complete and consistent ethogram be given, i.e. a set of m elements (behaviour patterns, acts or states), labelled by the index variable k, for k = 1.....m. It is then possible to record unambiguously the behavioural state of any individual at any instant of time. Let (k_{it}) denote the observation that individual i shows behaviour k at time t: t is a discrete time parameter, indexing the successively occurring behaviour states: (k_{i1}), $k(_{i2})$.....etc.; the real duration of the consecutive intervals may vary. Now $p(k_i)$ is the probability that subject i is currently (=t) showing behaviour k. These probabilities can be estimated from a sample of observed behaviour sequences. Associated with the probability distribution of current behaviour is the total information (in bits) as defined by the formula:

$$H(I_t) = - \sum_{k=1}^{m} p(k_i) \cdot \log_2 p(k_i) \qquad (1)$$

The unit of information is 1 bit. A bit is defined as the amount of information required for specifying one out of two equally probable outcomes. I_t is a random variable, denoting the state of individual i at a random moment of time, t; k_i denotes a particular value of this variable. Correspondingly, I_{t-1} is the random variable for the state of i at time t-1, that is, immediately preceding the state at time t. For nominal variables the information measure is equivalent to variance. We will denote $H(I_t)$ as total individual variability. For a second individual j,

the total variability of current behaviour is denoted as $H(J_t)$. The variability measure H is at a maximum when all m elements of the state set occur equally often; the maximum value of H is $\log_2 m$. The individual variability is at a minimum, i.e. zero, when just one element of the behavioural repertoire occurs during the whole period of observation. Thus, H measures the variability of an individual as manifested by the number of elements in his behaviour repertoire and the way he exhibits the elements in a sequence of behaviour. An increase or decrease in the H value can be interpreted as reflecting changes in "flexibility" or "rigidity" in the animal which is executing behavioural programs (on the functional significance of variability, see Conrad, 1977).

Autocovariability

Suppose that for individual i the occurrence of a given behaviour at time t is influenced by his immediately preceding behaviour at time t-1. It follows that there must be an intra-individual correlation between current and preceding behaviour, which can be measured by correlating the behaviour sequence with itself lagged one period. For the behaviour sequence of individual i we compare $(k_i t)$ with $(k_{i,t-1})$ for t=2, 3.....etc. The resulting measure of transmission is analogous to an autocorrelation index and will therefore be called autocovariability. It is based on intra-individual first-order behaviour transitions and is defined by the formula:

$$T(I_t:I_{t-1}) = H(I_t) + H(I_{t-1}) - H(I_t I_{t-1}) \qquad (2)$$

$H(I_t)$ and $H(I_{t-1})$ represent the total variability of the current behaviour of individual i (at time t) and its preceding behaviour (at time t-1). $H(I_t I_{t-1})$ is the variability of the combinations of preceding and following behaviour, that is, of the elements of the cartesian product IXI. The individual variabilities are computed from the marginal distributions in a contingency table containing preceding and subsequent behaviour. They tend to coincide as the length of the behaviour sequence approaches infinity and can therefore be regarded as virtually identical (for

sufficiently long sequences). Therefore, $T(I_t:I_{t-1}) = 2\,H(I_t) - H(I_t:I_{t-1})$. The autocovariability measures the degree to which an individual determines his own behaviour.

Cross-covariability

Suppose now that for individual i (the reference animal) the occurrence of a given behaviour at time t is influenced by the immediately preceding behaviour of another individual j. This inter-individual dependence is measured in the cross-covariability defined by the formula:

$$T(I_t:J_{t-1}) = H(I_t) + H(J_{t-1}) - H(I_tJ_{t-1}) \qquad (3)$$

$H(I_t)$ and $H(J_{t-1})$ are again individual variabilities, computed from marginal frequency distributions, in this case derived from a table containing combinations of the preceding behaviour of individual j and the subsequent behaviour of individual i. $H(I_tJ_{t-1})$ gives the variability of these combinations. Cross-covariability therefore measures the degree to which a partner determines the ongoing behaviour of the reference subject.

So far the development of our model somewhat parallels the models of Hazlett (1965) and of Dingle (1969), later refined by Conant and Steinberg (1973) and Steinberg and Conant (1974). These models are however restricted to interaction sequences in which the behaviours of the individuals i and j alternate or may be made to do so by inserting a dummy state for j between two acts of i. To the extent that this kind of interaction sequence is unrealistic (as is often the case with higher species such as primates) the problem arises of separating the influences originating from simultaneously acting sources. In our model, this problem is met by including a higher-order covariability term, reflecting a degree of interaction between the influences of the preceding behaviours of the reference individual and his partner. The decomposition we propose, namely the partition of the total sequential covariability $T(I_t:I_{t-1}J_{t-1})$ into three components, (a partial autocovariability component, $P(I_t:I_{t-1})$; a partial cross-covariability component $P(I_t:J_{t-1})$; and an interaction co-

variability, $P(I_t:I_{t-1}J_{t-1})$) eliminates a number of ambiguities in the information-measurement approach to interaction sequences as used by others (see chapter 5).

Interaction covariability

It is in theory possible that the influence from the preceding behaviours of the reference subject and that from its partner have exactly the same effect in terms of reducing the total variability in the current behaviour of the reference individual. This is the case when the behavioural states of i and j at time t-1 are perfectly correlated. Then $T(I_t:I_{t-1})$ and $T(I_t:J_{t-1})$ will be identical. This implies that whatever may be predicted from $(k_{i,t-1})$ and $(k_{j,t-1})$ can be predicted with complete accuracy from either $(k_{i,t-1})$ or $(k_{j,t-1})$ alone: we cannot determine which influence is responsible for a reduction in the variability of $H(I_t)$. On the other hand, it is also conceivable that the specific combination of both sorts of preceding behaviour provides additional information over and above the information contained in either of the preceding behaviours separately. In this case there is an effect on the variability in $H(I_t)$ which is not accounted for by the sum of the contributions of the separate predictors $(k_{i,t-1})$ and $(k_{j,t-1})$. In practice, the actual situation will normally fall in between these extremes: sometimes the influence from both preceding behavioural states will overlap and sometimes the specific combination will have an additional effect. The presence of an interaction term can be detected from a computation of the total sequential covariability, defined by:

$$T(I_t:I_{t-1}J_{t-1}) = H(I_t) + H(I_{t-1}J_{t-1}) - H(I_tI_{t-1}J_{t-1}) \qquad (4)$$

The term $H(I_{t-1}J_{t-1})$ represents the joint variability of the simultaneous behavioural states of i and j at time t-1 and is virtually equal to $H(I_tJ_t)$. The term $H(I_tI_{t-1}J_{t-1})$ represents the variability of the combination of the preceding states of i and j and of the current behaviour of the reference individual. The total sequential covariability measures the amount of mul-

tiple correlation between (I_t) and both (I_{t-1}) and (J_{t-1}). The autocovariability $T(I_t:I_{t-1})$ and the cross-covariability $T(I_t:J_{t-1})$ measure the correlation of (I_t) with (I_{t-1}) and (J_{t-1}) separately. To the extent that the preceding behaviours are not independent the total sequential covariability $T(I_t:I_{t-1}J_{t-1})$ will not equal the sum of the autocovariability $T(I_t:I_{t-1})$ and the cross-covariability $T(I_t:J_{t-1})$. It follows that the interaction covariability is defined as:

$$P(I_t:I_{t-1}J_{t-1}) = T(I_t:I_{t-1}) + T(I_t:J_{t-1}) - T(I_t:I_{t-1}J_{t-1}) \quad (5)$$

Depending upon the type of interaction effect present in the data, the interaction term has a positive or a negative sign, positive when the interaction effect is due to I_{t-1} or J_{t-1} negative when the effect is due to I_{t-1} and J_{t-1}. When the interaction term is positive, we cannot decide which source is responsible as each of them is sufficient and both of them are actually present. When the term is negative, we know that the actual combination of both sources is necessary for the effect. Depending on the sign of the interaction term, the partial covariabilities are greater or less than the transmission terms.

Although the total sequential covariability is similar to a multiple correlation coefficient, it is not quite an equivalent. Multiple correlation theory assumes a linear model, in which the correlation existing in a set of variables is broken down into a number of bivariate correlations; no higher order correlations are assumed. In multiple contingency theory, the total (sequential) covariability is broken down into a sum of bivariate (partial) covariabilities and a higher order term, which appears as an interaction effect. When interaction covariability is present, the influence of one variable on another differs according to the value of a third variable (in the analysis-of-variance this effect is subsumed under covariance).

Partial auto- and cross-covariability

The interaction covariability shows up as a residual term when the total sequential covariability cannot be fully accounted for

by the auto- and cross-covariability alone. When interaction is present, the auto- and cross-covariability terms as defined by the formulae (2) and (3) do not exclusively represent the effects on the current behaviour of the reference individual of his own previous behaviour of another's previous behaviour. Both influences have the interaction term in common. Therefore, to give appropriate weight to the relative importance of both influences we subtract the interaction term from the auto- and cross-covariability terms to derive an exclusive measure of the effects of the preceding behaviours of i and j. These terms are called partial autocovariability and partial cross-covariability:

$$P(I_t:I_{t-1}) = T(I_t:I_{t-1}) - P(I_t:I_{t-1}J_{t-1}) \quad (6a)$$

or

$$P(I_t:I_{t-1}) = T(I_t:I_{t-1}J_{t-1}) - T(I_t:J_{t-1}) \quad (6b)$$

and

$$P(I_t:J_{t-1}) = T(I_t:J_{t-1}) - P(I_t:I_{t-1}J_{t-1}) \quad (7a)$$

or

$$P(I_t:J_{t-1}) = T(I_t:I_{t-1}J_{t-1}) - T(I_t:I_{t-1}) \quad (7b)$$

In the case of simultaneously operating predictors, only the partial covariabilities measure the exclusive relationships of each predictor variable with the criterion variable. (A more exact notation would be $P_{J_{t-1}}(I_t:I_{t-1})$ and $P_{I_{t-1}}(I_t:J_{t-1})$, indicating which variable has been removed. To keep the notation simple however, we use P to indicate a partial covariability term with the understanding that the variables not occurring in the P-term have been eliminated.)

INTERPRETATION OF COVARIABILITY TERMS

It has been already mentioned that transmission or covariability measures can be interpreted as correlation indices. This is easy to understand when one realizes that the variability measure H is in fact a variance-like statistic (McGill, 1954, 1955; Garner and McGill, 1956). The difference between variance-statis-

tics and information statistics is that only the latter are appropriate for non-metric or categorical data. Just as the correlation coefficient between the variables X and Y is a function of the variance of their joint occurrences and of the single variances ($r_{xy} = \sigma_{xy}/\sigma_x\sigma_y$), the transmission between X and Y is also a function of their joint variability and the single variabilities: $T_{xy} = H_x + H_y - H_{xy}$ (cf. formula 2). The square of the correlation coefficient may be interpreted as the amount of variances in one of the single variables, say X, that can be accounted for by variation in the other variable Y. Analogously, the covariability between X and Y indicates the amount of variability in X that is due to variability in Y. In order to benefit from this relationship between variability and covariability, we may express the various covariability terms as a proportion of the total individual variability. The ratio of total sequential covariability and total individual variability, $T(I_t:I_{t-1}J_{t-1})/H(I_t)$, is therefore the amount of variability in I_t that can be ascribed to the effect of the predictors I_{t-1} and J_{t-1}. The contribution of a partial covariability can be evaluated by expressing it as a proportion either of the individual variability $H(I_t)$ or of the total sequential covariability $T(I_t:I_{t-1}J_{t-1})$. We prefer the latter normalization with the use of the following symbols and definitions:

normalized partial autocovariability

$$a_{ij} = \frac{P(I_t:I_{t-1})}{T(I_t:I_{t-1}J_{t-1})}$$

normalized partial cross-covariability

$$c_{ij} = \frac{P(I_t:J_{t-1})}{T(I_t:I_{t-1}J_{t-1})}$$

and normalized interaction covariability

$$x_{ij} = \frac{P(I_t:I_{t-1}J_{t-1})}{T(I_t:I_{t-1}J_{t-1})}$$

When the partial covariabilities and the interaction covariability have been defined by the formulae (5), (6b) and (7b), the

sum of the normalized covariabilities is equal to 1. When j is taken as the reference subject the corresponding terms are a_{j1}, c_{j1} and x_{j1} respectively.

Up to this point we have dealt with the following levels of description and interpretation. Data, particularly of interaction sequences, is described by certain informational statistics: variabilities and (partial) covariabilities. To the extent that these parameters are the terms of a structured model for the data, they can be interpreted within the model: when covariabilities are related to the variability of a dependent variable, they are said to explain - in a statistical sense - a part of that variability because they identify a source of it. A further level of interpretation is reached when we consider that variabilities describe behaving individuals and when we consequently interpret an observed covariability as representing or reflecting a property of the behaving subjects. We can then interpret the covariability between i and j, representing the influence of i on j, as an effect due to a property of i (or of j). An example of this type of reasoning is the identification of "communication between animals" and "cross-covariability in interaction sequences". Further examples will be given in chapter 7.

SUMMARY OF THE MODEL

Using the covariability measures defined in the previous section we were able to formulate a structural model for dyadic interactions based on first-order intra-individual and inter-individual behavioural transitions. The model may be cast in the following equation:

$$H(I_t) = P(I_t:I_{t-1}) + P(I_t:J_{t-1}) + P(I_t:I_{t-1}J_{t-1}) + U(I_t) \qquad (8)$$

This equation summarizes the factors contributing to the occurrence of consecutive behavioural states in a reference individual, as manifested by particular components of variability. The sequence of consecutive behavioural states is characterized by an overall variability, expressing the uncertainty of each subse-

quent behaviour pattern. This variability or uncertainty is reduced by taking into account the various sources affecting the occurrence of the subsequent behaviour. Expressed in informal terms, equation (8) can be described as follows. When an individual decides on his behaviour to follow, he takes account of his own preceding behaviour, thereby reducing the uncertainty of his subsequent benaviour by a certain amount, which is measured as the partial autocovariability, $P(I_t:I_{t-1})$. He also considers the preceding behaviour of his partners, which again reduces the unpredictability of his subsequent behaviour by a certain amount, the partial cross-covariability $P(I_t:J_{t-1})$. Furthermore, he considers whether the specific combination of the preceding acts involves additional information or a reduction of uncertainty: this interaction covariability is measured as $P(I_t:I_{t-1}J_{t-1})$. A degree of unpredictability may of course still remain, at least for the external observer, who does not know whether the identified sources are the only ones involved; this uncertainty is indicated by the term $U(I_t)$.

In formal terms, equation (8) represents an analysis-of-variance model: the variability of the ongoing behaviour of subject i can be broken down into partial components for his own preceding behaviour and for the preceding behaviour of others, an interaction component, and, possibly, a remainer or residual term. As long as no restrictions are imposed on the values of the parameters, equation (8) represents a whole class of models. It can be applied to an observed set of data in an exploratory way, to investigate whether its structure is at all realistic. The model of equation (8) is clearly appropriate when the unexplained or residual variability is significantly smaller than the total sequential covariability.

The model has three variables: the current behaviour of the reference subject (I_t), the preceding behaviour of the reference subject (I_{t-1}), and that of his partner (J_{t-1}). The current behaviour of the reference subject is taken as the dependent or criterion variable; its variability is to be explained by its relationship with the other two variables (Fig. 4.1). The only terms of interest, therefore, from the full set of terms de-

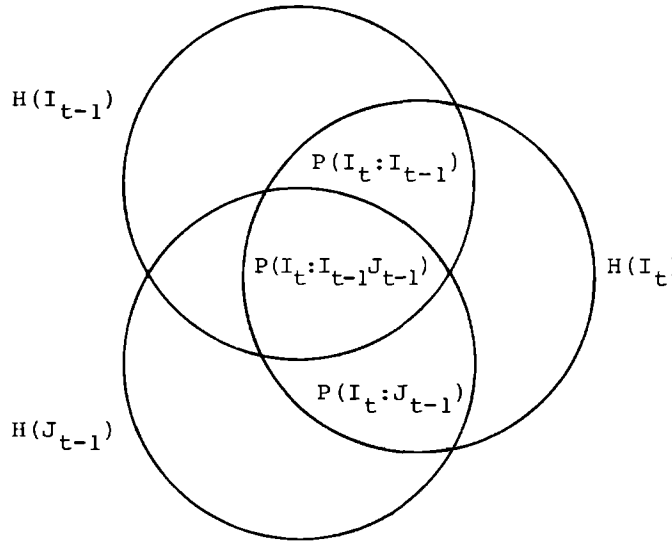


Fig. 4.1

Venn diagram identifying the parts of the variability of the ongoing behaviour of a reference subject i that are due to the preceding behaviour of i, to the preceding behaviour of j, and to the specific combination of these variables.
$P(I_t:I_{t-1})$ = partial autocovariability
$P(I_t:J_{t-1})$ = partial cross-covariability
$P(I_t:I_{t-1}J_{t-1})$ = interaction covariability

scribing all possible relationships between the three variables, are the terms containing a part of the single variability $H(I_t)$, viz. the partial autocovariability, the partial cross-covariability, the interaction covariability and the residual variability. These terms are called the model parameters, which are to be estimated from the data parameters directly characterizing the observations, viz. the single variabilities $H(I_t)$, $H(I_{t-1})$, $H(J_{t-1})$ and the joint variabilities $H(I_tI_{t-1})$, $H(I_tJ_{t-1})$, $H(I_{t-1}J_{t-1})$ and $H(I_tI_{t-1}J_{t-1})$. It is evident from Fig. 4.1 that a combination of the data parameters by addition and subtraction will result in the desired model parameters.

Specific details of the computational procedure are given in chapter 8.

EXAMPLES

The meaning of the various informational statistics discussed in the previous sections may be illustrated by the following examples. Let us take the simplest case: the situation of dyadic interaction between two individuals, i and j, which can both be in one of two states, 1 or 2. Let the variables I_t, I_{t-1} and J_{t-1} be defined as above: I_t is the current behaviour of i (= 1 or 2), I_{t-1} is the previous state of i (also 1 or 2) and J_{t-1} is the previous state of j (again 1 or 2). I_{t-1} and J_{t-1} are taken as the predictors for the criterion variable I_t. The $2^3 = 8$ different combinations of values of the variables I_t, I_{t-1} and J_{t-1} are listed in Table 4.1. Let us suppose that we have obtained the (relative) frequencies of each of the 8 state-combinations as indicated in the second column of Table 4.1. From these joint frequencies all the required single and joint variabilities can be computed. For the sake of clarity, however, we will represent the data in the form of two separate transition matrices (one for the transitions within i, and one for the transitions between j and i) and one contingency table (for the combined occurrences of the predictors), as shown in Table 4.2. The procedure is as follows. From Table 4.1 we can compute the total joint variability $H(I_tI_{t-1}J_{t-1})$ according to formula (1) as 2.3842 bits. From the marginal distributions of the matrices in Table 4.2 we obtain: $H(I_t) = 0.9709$ bits, $H(I_{t-1}) = 0.9709$ bits and $H(J_{t-1}) = 0.8813$ bits. Since the distribution for I_t,(60, 40), is more random than the distribution for J_{t-1},(70, 30), its variability is correspondingly larger. The matrices in Table 4.2 also provide the joint variabilities for the pairs of variables; $H(I_tI_{t-1}) = 1.8395$ bits, $H(I_tJ_{t-1}) = 1.7610$ bits, and $H(I_{t-1}J_{t-1}) = 1.6010$ bits. From these parameters the following transmissions or covariabilities can be obtained:

TABLE 4.1

The possible values for the combination of three two-state variables and their (hypothetical) frequency distribution

combination			frequency
I_t	I_{t-1}	J_{t-1}	
1	1	1	40
1	1	2	5
1	2	1	10
1	2	2	5
2	1	1	15
2	1	2	0
2	2	1	5
2	2	2	20

TABLE 4.2

Contingency tables of frequencies for pairs of variables (derived from the data in Table 4.1)

intra-individual transitions			inter-individual transitions			predictor combinations		
I_{t-1} :	I_t		J_{t-1} :	I_t		I_{t-1} :	J_{t-1}	
	1	2		1	2		1	2
1	45	25	1	50	20	1	55	5
2	15	25	2	10	20	2	15	25

$T(I_t:I_{t-1})$	0.1023 bits		(formula 2)
$T(I_t:J_{t-1})$	0.0912 bits		(formula 3)
Total		0.1935 bits	
$T(I_t:I_{t-1}J_{t-1})$		0.1877 bits	(formula 4)
$P(I_t:I_{t-1}J_{t-1})$		0.0058 bits	(formula 5)

The separate contributions of the predictors are virtually equal to the total sequential covariability; the relationship between the predictors does apparently not affect the relationship between each of them and the criterion.

A number of borderline cases illustrating the relationships between the variables I_t, I_{t-1} and J_{t-1} will also be shown. In Table 4.3 a number of distributions for the joint variable $(I_tI_{t-1}J_{t-1})$ are given, together with the corresponding parameters for the breakdown of the criterion variability. To facilitate interpretation, Table 4.4 shows the same data in the form of bivariate contingency tables. In case I each of the bivariate contingency tables contains a completely random distribution; in cases II, III and IV, two of the bivariate distributions are random and the third one is perfectly correlated; in case V all of the bivariate contingency tables contain perfectly correlated variables. Let us first consider the cases II, III and IV. They are formally equivalent: perfect correlation between one pair of variables and no correlation in the remaining pairs. From the point of view of the criterion variable I_t however the cases show a difference. In case II the predictors (which are perfectly correlated) do not contribute to the criterion variability at all. In cases III and IV there is total sequential covariability of 100%, i.e. the criterion variable is in each case fully determined by one of the predictors; the other predictor is uncorrelated with either the first predictor or the criterion: there is therefore only one partial covariability term in each case and no interaction term. Case V represents the situation with perfect correlation in every pair of variables leading to total (100%) sequential covariability; none of the predictors is alone in contributing to the criterion variability and the whole of the sequential covariability

TABLE 4.3

Various borderline cases illustrating the relationships between three variables as appearing in the joint frequency distribution of the variables, and their consequences for the decomposition of the criterion variability

I_t	I_{t-1}	J_{t-1}	I	II	III	IV	V
1	1	1	25	25	25	25	50
1	1	2			25		
1	2	1				25	
1	2	2	25	25			
2	1	1		25			
2	1	2	25			25	
2	2	1	25		25		
2	2	2		25	25	25	50
$H(I_t)$			1	1	1	1	1
$T(I_t:I_{t-1}J_{t-1})$			1	0	1	1	1
$P(I_t:I_{t-1})$			1	0	1	0	0
$P(I_t:J_{t-1})$			1	0	0	1	0
$P(I_t:I_{t-1}J_{t-1})$			- 1	0	0	0	1

is a result of interaction covariability. In case I the predictors I_{t-1} and J_{t-1} are neither correlated with the criterion variable I_t, nor with each other. The total sequential covariability of 1 bit (= 100%) can only be due to the specific combination of the predictors; all of the total sequential goes into the negative interaction term.

To illustrate the meaning of the interaction term further, two additional cases that are more realistic, are shown in Tables 4.5 and 4.6.

TABLE 4.4

Contingency tables for pairs of variables, derived from the data in Table 4.3

	intra-individual transitions		inter-individual transitions		predictor combinations	
	I_{t-1}	: I_t	J_{t-1}	: I_t	I_{t-1}	: J_{t-1}
I	25	25	25	25	25	25
	25	25	25	25	25	25
II	25	25	25	25	50	0
	25	25	25	25	0	50
III	50	0	25	25	25	25
	0	50	25	25	25	25
IV	25	25	50	0	25	25
	25	25	0	50	25	25
V	50	0	50	0	50	0
	0	50	0	50	0	50

TABLE 4.5

Hypothetical joint frequency distributions for three two-state variables

I_t	I_{t-1}	J_{t-1}	VI	VII
1	1	1	30	30
1	1	2	5	5
1	2	1	5	5
1	2	2	10	10
2	1	1	10	0
2	1	2	5	15
2	2	1	5	15
2	2	2	30	20

TABLE 4.6

Contingency tables for pairs of variables corresponding to the data in Table 4.5

	intra-individual transitions		inter-individual transitions		predictor combinations	
	I_{t-1}	: I_t	J_{t-1}	: I_t	I_{t-1}	: J_{t-1}
VI	35	15	35	15	40	10
	15	35	15	35	10	40
VII	35	15	35	15	30	20
	15	35	15	35	20	30

The single and joint variabilities for cases VI and VII and the corresponding model parameters are as follows:

$H(I_t)$	1		1	
$H(I_{t-1})$	1		1	
$H(J_{t-1})$	1		1	
$H(I_tI_{t-1})$	1.88		1.88	
$H(I_tJ_{t-1})$	1.88		1.88	
$H(I_{t-1}J_{t-1})$	1.72		1.97	
$H(I_tI_{t-1}J_{t-1})$	2.57		2.57	
$T(I_t:I_{t-1})$	0.12		0.12	
$T(I_t:J_{t-1})$	0.12		0.12	
Total		0.24		0.24
$T(I_t:I_{t-1}J_{t-1})$		0.15		0.40
$P(I_t:I_{t-1}J_{t-1})$		0.09		- 0.16

In case VI each of the predictors is highly correlated with the criterion variable. Moreover, the predictor variables also correlate highly. As a consequence the total sequential covariability can be broken down into two partial covariabilities and a positive interaction term that represents a redundancy effect. The predictors duplicate each other in the prediction of the criterion, which becomes manifest as a positive interaction effect. Case VII is similar in that the correlations between the predictors and criterion variable is high; but the predictors are not correlated with each other in the same way as each of them with the criterion; they are, in fact, associated more loosely with each other than with the criterion. The result is that their combination can have a true interaction effect, which becomes manifest in the form of a negative interaction term.

COMMENT ON TERMINOLOGY

There is no uniform terminology for information-theoretical statistics. McGill (1955) and Garner (1962) promoted their use in the analysis of multivariate categorical data and developed a set of appropriate terms. Applications in ethology, however, often retained the connotation of information transmission as used in the analysis of communication channels. To facilitate cross-referencing we present below a short list of equivalent terms.

The H-measure for a probability distribution is variously called a measure for "entropy", for "information", for "(un)-predictability", for "uncertainty", or for "variability". The association between two or more variables was originally called "transmission of information" or "transinformation". In data analysis it is called "contingent uncertainty" (Garner, 1962), "constraint" (Broekstra, 1978), simply "correlation" (Watanabe, 1960) or "covariability". In the terminology of our three-variable situation we attempted to retain the notions that the variables identified as predictors precede the criterion variable in time and that prediction is based on intra- and inter-individual transitions of behaviour: the terms partial, auto- and cross-covariability are more specific than the term partial contingency, as used by Garner (1962).

One final comment must be made on the definition and interpretation of the interaction term. Garner (1962) offers a derivation that is somewhat different to ours (Garner, 1962, pp. 101-110; in particular his formula 4.7). As a result his definition is as follows (in our notation):

$$P(I_t:I_{t-1}J_{t-1}) = T(I_t:I_{t-1}J_{t-1}) - T(I_t:I_{t-1}) - T(I_t:J_{t-1}) \qquad (5')$$

This definition gives an opposite sign to the difference between the total sequential covariability and the sum of the separate covariabilities. Whenever this definition is substituted in our formulae certain additional changes in sign should be made. In particular, our equation (8) would become:

$$H(I_t) = P(I_t:I_{t-1}) + P(I_t:J_{t-1}) - P(I_t:I_{t-1}J_{t-1}) + U(I_t) \quad (8')$$

The total sequential covariability in our model consists of the partial covariabilities plus the interaction term. In Garner's formulation it would consist of the partial covariabilities, minus the interaction term. Furthermore, in Garner's version the conditions for a positive or negative interaction term are reversed: a negative interaction term results from a correlation between the predictors (Garner, 1962, pp. 106-107).

CHAPTER 5

OTHER INFORMATION-STATISTICAL MODELS FOR INTERACTION SEQUENCES

The use of information-statistics in the analysis of interaction sequences may serve various aims. Our model is designed to explain an animal's present behaviour by relating it to its behavioural history; the residual variability plays an important role in judging the success of this attempt. Previous ethological models have however been primarily focussed on communication between individuals, the relevant measure being the cross-covariability. Conceptually, it is quite possible to study merely the influence of J_{t-1} on I_t and disregard other effects, e.g. that of I_{t-1}. One should realize however that the cross-covariability between J_{t-1} and I_t cannot always be exclusively interpreted as communication. The existing models of communication will be briefly summarized. To facilitate comparison we will treat them as though it were intended that they account for the variability of ongoing behaviour by relating this to communicative effects. Every model breaks down the individual variability $H(I_t)$ into a number of components associated with particular predictor variables and a residual term, $U(I_t)$, (which can have a different value in each model).

Altmann

The basic idea of Altmann's model is that ongoing behaviour of a reference subject in a social situation can be exclusively explained in terms of the preceding behaviours of other individuals. Altmann proposes the fitting of a set of Markov models of successively higher order to the data. It is firstly assumed that the total variability of the behaviour of a reference subject i results from the influence of the immediately preceding behaviour of another individual j; if this first-order model is inadequate, a second-order model is assumed, which hypothesises that there is additional influence from the next preceding behaviour of others; where once again this model does not adequately account for the variability of individual i, the next preceding behaviour again is also tested as a predictor (the "other individual j" in this series of models need not to be the same in each period!). Altmann concludes from his data that a third-order model is adequate, in other words, inclusion of three previous behaviours of "j" accounts for most of the variability of i's current behaviour. Altmann's model is therefore a four-variable lagged model with one variable (I_t) as the criterion variable and three predictors: J_{t-1}, J_{t-2} and J_{t-3}. Reformulating it as a minimum analysis-of-variance model and retaining the same residual term $U(I_t)$ it may be represented as:

$$H(I_t) = T(I_t:J_{t-1}J_{t-2}J_{t-3}) + U(I_t) \qquad (9)$$

Equation (9) simply states that a given individual's current behaviour is a lagged function of other individuals' behaviour in three preceding periods. When applied to interaction sequences to measure communication between individuals, it is necessary to ensure that the term $T(I_t:J_{t-1}J_{t-2}J_{t-3})$ does indeed represent inter-individual effects only. This question of ambiguity is independent of the analytical framework of equation (9): $T(I_t:J_{t-1}J_{t-2}J_{t-3})$ can be interpreted either as the total sequential constraint generated in a third-order Markov process or as the total of the constraints imposed on I_t by the preceding behaviours J_{t-1}, J_{t-2} and J_{t-3} separately. (In the simplest

ANOVA case these constraints consist of only three main effects.) There are therefore two questions to be discussed below: what does $T(I_t:J_{t-1}J_{t-2}J_{t-3})$ effectively measure and how is it to be interpreted?

Hazlett and Bossert, Dingle, Conant and Steinberg

These models have already been mentioned and the difference between them is not essential to the argument; they do not allow for interaction effects, although the interaction term that is omitted differs in each case. In comparison to Altmann's the models are relatively simple and direct. Hazlett and Bossert first identify communication with inter-individual first-order covariability: $T(I_t:J_{t-1})$; then they attempt to detect the possible influence of "context" (represented by the behaviour, I_{t-2}, which preceeds the communicative event $J_{t-1}I_t$) by considering the three-act sequences: $I_{t-2}J_{t-1}I_t$. As long as the interactants are behaving in an alternating manner, the transmission $T(I_t:J_{t-1})$ will not be upset by influences from I_{t-1}, as this variable does not occur in the sequence. It is however affected by a possible interaction effect from I_{t-2}; the covariability $T(I_t:J_{t-1})$ does not exclusively reflect the effect of J_{t-1}, since the covariance has not been partialled out. The required interaction term is $P(I_t:J_{t-1}I_{t-2})$. The model for communication as proposed by Hazlett and Bossert, without regard to context, becomes:

$$H(I_t) = T(I_t:J_{t-1}) + U(I_t) \qquad (10)$$

When the context is included (i.e. the behaviour preceding the actual instance of communication), the model is:

$$H(I_t) = T(I_t:J_{t-1}) + P(I_t:I_{t-2}) + U(I_t) \qquad (11)$$

(Note: when $P(I_t:I_{t-2}) \neq 0$, $U(I_t)$ in equation (11) will have a value differing from $U(I_t)$ in equation (10))

This model has also been used, for alternating sequences, by Lehman and Adams (1977) who called the effects of context "indirect, 'reflected' effects".

Dingle's model is intended to represent inter-individual influences (communication) as well as intra-individual influences in first-order transitions. However, the covariabilities $T(I_t:J_{t-1})$ and $T(I_t:I_{t-1})$ are affected by the interaction effect $P(I_t:I_{t-1}J_{t-1})$.

Conant and Steinberg use the same model but apply it differently, retaining the identity of the interactants in the data. The combinations $(I_{t-1}J_t)$ and $(J_{t-1}I_t)$ are kept distinct, whereas Hazlett and Bossert and also Dingle regard both types of transition as instances of one "actor-respondent" interaction. Although Conant and Steinberg stress the importance of "self communication" (autocovariability) they do not fully separate it from inter-individual communiation. Their model is simply:

$$H(I_t) = T(I_t:I_{t-1}) + T(I_t:J_{t-1}) + U(I_t) \qquad (12)$$

Marko, Hauske and Neuburger

This model too incorporates only cross-covariability effects, but the authors develop a different rationale for the identification of social interaction and empirical correlations. Their reasoning is as follows: the notion of causality implies that cause and effect cannot be coincident in time; therefore, correlation between simultaneous events cannot be due to causal interaction between these events, so that any correlation existing between simultaneous events has to be accounted for by factors preceding these events. Specifically, any correlation between the behavioural states of subjects i and j at time t has to be due to the influence of the preceding states of both i and j. Marko and Neuburger regard the correlation between (I_t) and (J_t) as an index of the net result of communication originating from previous behavioural acts. They continue by developing a mathematical method to separate the contribution of each next preceding behaviour of both i and j to this correlation. The general idea of their model may be formulated as follows:

$$H(I_t) = T(I_t:J_t) + U(I_t) \qquad \text{where} \qquad (13)$$

$$T(I_t:J_t) = P(I_tJ_t:I_{t-1}) + P(I_tJ_t:I_{t-2}) \ldots\ldots + P(I_tJ_t:I_{t-n}) + P(I_tJ_t:J_{t-1}) + P(I_tJ_t:J_{t-2}) \ldots\ldots + P(I_tJ_t:J_{t-n}) \quad (14)$$

The proportion of the total variability of a reference individual accounted for by communication processes is limited to the correlation existing between the ongoing behaviour of i and j, as expressed in equation (13). The model is valid for situations that can be represented by two coupled stochastic processes, each with Markov properties. The terms on the right hand side of equation (14) are called "directed transinformations" and constitute the coupling or covariability of I_t and J_t. Marko's model was applied by Mayer (1971) in a study on social interaction in squirrel monkeys. Another application can be found in Hauske and Neuburger (1968).

Other applications of information theory

Several studies of social interaction combine the data-analytical framework of numerical taxonomy (Sneath and Sokal, 1973), and the formalism of information theory, into a technique called character analysis (Hazlett and Estabrook, 1974a, b), reviewed by Steinberg (1977). It is used to analyse any social interaction between two or more animals that can be described by alternating sequences. The method does not breakdown polyadic interaction sequences into pairs of dyadic sequences, and has to cope with substantial computational complexities in the case of larger repertoire sizes.

Finally, a procedure used by Baylis (1976) should be mentioned. He observed that courtship behaviour in cichlids could not be neatly described by alternating sequences and he decided to treat the male-female pair as a single channel source. The data are represented in one transition matrix where half the rows contain the preceding behaviour of the male and half those of the female; the subsequent behaviour is similarly entered in different columns for male and female. Although Baylis did not use an analysis-of-variance approach, his data represent exactly the situation for which it is appropriate.

Confounding of effects

The analysis-of-variance metaphor offers the opportunity to point out a general characteristic of the models outlined above, namely the confounding of several effects in one data parameter. This is mostly due to the fact that the primary aim of the models was to measure communication between individuals and to the assumption that inter-individual transmission is appropriate for that purpose. The assumption that inter-individual cross-covariability (in Altmann's case extended over third-order transitions) is due to and represents communication can be shown to be unfounded. If we suppose that the effect of communication between individuals does indeed show up in covariability measures, then it does not follow that any cross-covariability adequately measures communication. The latter supposition would follow only if there were no intra-individual sequential constraints, measured in the autocovariability term. Now, Altmann's study did not empirically exclude the presence of this term; in fact, he did not look for it at all. If autocovariability is indeed present, the observed cross-covariability misrepresents the effect really due to communication. This can easily be seen from Fig. 5.1. If we identify one of the predictors as representing the preceding behaviour of the reference subject, e.g. variable 3, we have a model in which I_{t-1} (= variable 3), J_{t-1} (= variable 1), and J_{t-2} (= variable 2) are supposed to contribute to the variability of the reference subject, I_t (= variable 0). The total sequential covariability between the predictors (J_{t-1} = 1; J_{t-2} = 2, and I_{t-1} = 3) and the criterion (I_t = 0) has been indicated by the hatched areas, the parts labelled 01, 02, 03, 012, 013, 023 and 0123. The cross-covariability between the current behaviour of the reference subject (I_t = 0) and the preceding behaviours of other individuals (J_{t-1} = 1 and J_{t-2} = 2) consists of the diagonally hatched areas, the parts 01, 02, 012, 013, 023 and 0123. The autocovariability between I_t and I_{t-1} comprises the parts 03, 013, 023 and 0123. The total sequential covariability can, at least theoretically, be broken down into components for the exclusive influence of each of the predictors (the parts 01 and 02) and a partial auto-

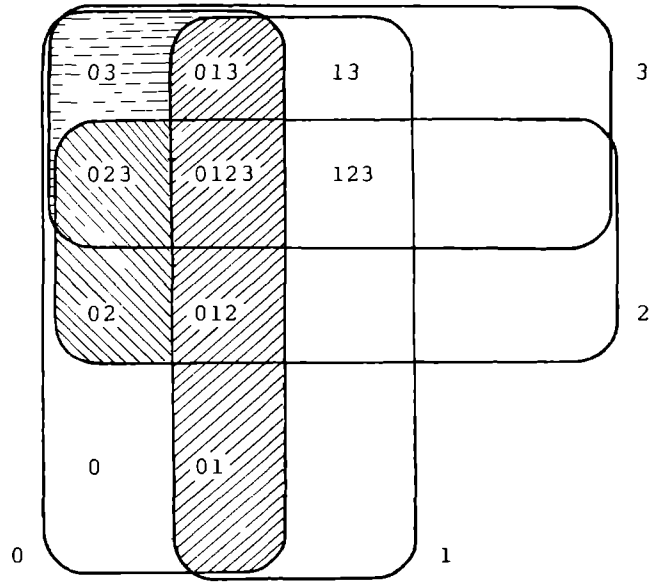


Fig. 5.1

Venn diagram of the covariability relationships between four variables: 0, 1, 2, and 3

covariability (03); the remaining parts of the total sequential covariability consist of effects of combinations of predictors, i.e. higher-order covariabilities. Without empirical testing it cannot be asserted that the latter are zero. In the cross-covariability (01, 02, 012, 013 and 0123) the exclusive influence of others is confounded by the parts 013, 023 and 0123. This ambiguity is much more serious when one retains Altmann's original three predictors, J_{t-1}, J_{t-2} and J_{t-3}, but cannot exclude *a priori* autocovariability effects from I_{t-1} and perhaps even from I_{t-2} and I_{t-3}.

The lack of discrimination between effects is much less serious in the two- or three-variable models used by Hazlett and Bossert, Dingle, and Conant and Steinberg. By reference to Fig. 4.1 it can be seen that by taking the cross-covariability term as a measure

of communication, the amount of communication by the term $P(I_t:I_{t-1}J_{t-1})$ is misrepresented. The same criticism applies to a similar model presented for general data analysis by Char-Tung-Lee (1971).

As far as Marko's model is concerned, there is no confounding in the strict sense. Marko was only interested in inter-individual effects and these are accounted for by two directed transinformations. Consider the relationships between the preceding and subsequent behaviours of two individuals i and j. Marko analyses the correlation between I_t and J_t into two components, one representing the contribution by I_{t-1} and the other the effect of J_{t-1}. The same preceding behaviours give rise to the partial cross-covariabilities, $P(I_t:J_{t-1})$ and $P(J_t:I_{t-1})$, which can also be interpreted as representing communication. In the special case of two coupled Markov chains the directed transinformations and the partial cross-covariabilities are equal. The question then arises of how to decide between models. As well as goodness of fit with respect to individual variability, other considerations must be taken into account, e.g. the different theoretical interpretations conveyed by the frameworks of Markov models and ANOVA analogy. This difference becomes especially important in the case of higher order sequential dependencies.

The analytical framework of information-statistical models

Without loss of generality, let us suppose that we are dealing with the situation that Altmann assumed, namely behavioural interaction sequences that can be adequately covered by unambiguous third-order inter-individual contingencies. This situation can be interpreted in terms of a third-order Markov model or in ANOVA terms. This will be illustrated by reference to the four-variable case in Fig. 5.1. Variable 0 is the dependent variable again and the variables 1, 2, and 3 are taken as independent variables. In a fully specified analysis-of-variance model there are three main effects exclusively due to each of the three independent variables, the effects of variable 1 on variable 0, of 2 on 0 and of 3 on 0, which are labelled as the parts 01, 02 and 03 in Fig. 5.1 respectively; three first-order interaction effects originating from all pairwise combinations of the predictors: 012, 023 and

013; one second-order interaction effect due to the specific combination of the predictors: 0123; and the residual variability escaping the predictors: 0. The logic of this breakdown of the dependent variability was of course not Altmann's: he applied the logic of a (third-order) Markov model, resulting in only three covariability terms, together constituting the total sequential constraint in the sequence, $T(I_t:J_{t-1}J_{t-2}J_{t-3})$, (hatched areas in Fig. 5.1). Only the residual variability is the same in both cases. This means that the models are really alternative statistical descriptions of the dependent variable, even if their explanatory power, as measured by the residual variability, is the same. A model must be judged not only by its goodness of fit, but also by the meaningfulness of its terms.

It can be argued that the terms, with which the residual variability is lowered when successive steps are added in fitting higher order Markov models, are not usually separately interpreted. In that case the Markov model would have the merit of mathematical simplicity: one single term, $T(I_t:J_{t-1}J_{t-2}J_{t-3})$, representing the influence of an animal's behavioural history on its current behaviour. At the same time it would however have the disadvantage of being psychologically rather unattractive. When ongoing behaviour is a function of a combination of immediately preceding acts, all possible sequential associations must either be pre-programmed in the nervous system or be learned in accordance with the principles of conditioning. In both cases a heavy burden is placed on the nervous system (compare the arguments against Markov models for language in Miller et al., 1960 and Miller and Chomsky, 1963; Altmann, 1965, acknowledges the problem for behaviour in general). On the other hand, an analysis-of-variance separates by definition the contributions of several preceding acts into additive effects; such a model would be appropriate if the selection of current behaviour were not based on a combination of preceding acts as a whole but depended indeed on a consideration of the preceding behaviours separately.

It must be emphasized that this discussion is purely theoretical. It is simply not known how animals actually relate their current behaviour to their behavioural history. When sequential

constraints are observed that can be described equally well within the framework of either Markov processes or an analysis-of-variance, the choice between models has to depend on additional information (theoretical considerations and empirical data). The point to note from this discussion is that the same information-theoretical statistics, applied to data in a descriptive way, can be differently interpreted when the statistics are arranged in different frameworks. Information-theoretical statistics can appear in at least three different contexts: those of Markov processes, of analysis-of-variance, as discussed above, or of character analysis (Steinberg, 1977). Each framework permits its own class of structural models and conveys its own interpretation. Moreover, for each framework to be applicable, its own set of conditions is required, e.g. stationarity. (For a criticism of the Markovian nature of Altmann's approach see Metz, 1974; also additional comments in Cane, 1978). Ethological theory on the overall organization of ongoing behaviour is at present not sufficiently well developed to guide data analysis and hypothesis testing (but see Sibly and McFarland, 1976).

Complete models in comparison with reduced models

In order fully to analyse the interaction between two subjects i and j, the models discussed above have to be applied twice: both i and j have to be tested as the reference subject. One might argue that the proper representation of dyadic interaction would be a model with two criterion variables, I_t and J_t, and a set of predictors (varying in each model). A complete representation of the relevant variables however has no logical or interpretational advantage over the reduced representation and merely increases the computational complexity. The complete (four-variable) representation of the interaction between two subjects, i and j, as manifested in first-order inter- and intra-individual transitions, would contain the following variables: the current behaviours of i and j (I_t and J_t respectively), and the preceding behaviours of i and j (I_{t-1} and J_{t-1}). Let us once again refer to Fig. 5.1 and interpret it now as representing the relationships between two criterion variables and two independent variables.

Let us further identify the variables 0 and 1 as I_t and J_t respectively and the variables 3 and 2 as I_{t-1} and J_{t-1}. In the reduced (three-variable) representation as shown in Fig. 4.1, the criterion variability is divided into four terms: three partial covariabilities and one residual variability, all four of theoretical interest. The four-variable model breaks down the criterion variability into eight terms; all of the four original terms are now further divided as a result of the fact that the current behaviours of i and j are correlated. For instance, the original term for autocovariability is divided into the parts labelled 03 and 013. This division is of no particular interest however. The term 013 stands for that part of i's current behaviour (variable 0) that is correlated with his own preceding behaviour (variable 3), and at the same time with j's current behaviour (variable 1). We can regard this division as a consequence of the fact that i and j's current behaviours happen to be correlated. We are primarily interested in the relationship between the behavioural history of a subject and his current behaviour; in the data this relationship corresponds to the correlation between preceding and subsequent behaviours, e.g. the autocovariability (the parts 03 and 013 in Fig. 5.1). Subdivision may be possible, but it falls outside the scope of our study.
A Marko-Neuburger line of reasoning might however capitalize on this, interpreting the term 013 as that part of the correlation between I_t and J_t (variables 0 and 1) conceived as "communication" between i and j, that is specifically due to I_{t-1} (variable 3). But this begs the question of the treatment of first-order effects; e.g. 13, representing part of the cross-covariability between J_t and I_{t-1}. A similar argument applies to the subdivision of the other terms of the three-variable model: in the context of the relationships under study this appears to be irrelevant. (Note: the subdivision of the covariability between i and j's current behaviours as indicated in Fig. 5.1 is in fact not equivalent, but merely analogous, to that of the Marko-Neuburger model as formulated in equation 13).

A comparative assessment of information-statistical models

The models proposed in the literature on animal communication differ in what they attempt to measure, in their rationale and in their complexity. Table 5.1 gives their defining equations together with the computational formulae for the residual variability. In order to develop an informational model for the analysis of social interaction, particularly for communicative behaviour, such as is assumed to be present in observed interaction sequences, the following points must be settled. Firstly, what kind of components can occur and which of them are of interest (e.g. autocovariability or cross-covariability)? Secondly, what kind of analytical framework is to be preferred (e.g. that of Markov models or of analysis-of-variance)? Finally, what is an appropriate level of complexity (e.g. first-order, higher-order transitions)?

The structural properties of the information-statistical models discussed in the previous sections are summarized in Table 5.2 (and Fig. 6.1). Model II is rather complex as far as the number of variables and sequential order is concerned, and neglects autocovariability and interaction. Model III contains terms comparable to those in model IV, but its rationale bypasses a direct interpretation of first-order intra- and inter-individual transmissions. Model IV is at the same time parsimonious with respect to the number of variables and sequential order and complete as to the effects identified. It is however, both in the special case of alternating behaviour, and where interaction effects are definitely absent, identical to model I. An empirical comparison of these models as applied to data on the social interaction of Java-monkeys is given in the next chapter.

Complexity of social interaction vs complexity of models

The degree of structural complexity associated with any multivariate model of interaction sequences does not often fully reflect the variety of relationships known or assumed to be present in the data. When a combination of several variables is assumed to be causally related to a criterion variable several main effects and interaction terms can arise. The point to note is that

TABLE 5.1

Information statistical models of social interaction

Model	Structural formula
I	$H(I_t) = T(I_t{:}J_{t-1}) + U(I_t)$
II	$H(I_t) = T(I_t{:}J_{t-1}J_{t-2}J_{t-3}) + U(I_t)$
III	$H(I_t) = T(I_t{:}J_t) + U(I_t)$
IV	$H(I_t) = P(I_t{:}I_{t-1}) + P(I_t{:}J_{t-1}) + P(I_t{:}I_{t-1}J_{t-1}) + U(I_t)$

Model	Computational formula for residual variability
I	$U(I_t) = H(I_tJ_{t-1}) - H(J_{t-1})$
II	$U(I_t) = H(I_tJ_{t-1}J_{t-2}J_{t-3}) - H(J_{t-1}J_{t-2}J_{t-3})$
III	$U(I_t) = H(I_tJ_t) - H(J_t)$
IV	$U(I_t) = H(I_tI_{t-1}J_{t-1}) - H(I_{t-1}J_{t-1})$

H = variability of behaviour or of combination of behaviours
T = transmission or covariability between behaviours
P = partial covariability between behaviours
U = residual variability
I_t, I_{t-1}, J_t, J_{t-1} = *current and preceding behaviours of i and j respectively*
(the models I-IV are graphically represented in Fig. C.1)

TABLE 5.2

Comparison of structural properties of information-statistical models of interaction sequences and communication (= cross-covariability)

model	authors	number of variables	sequential order	terms of interest	confounded terms
I	Hazlett-Bossert Dingle Conant-Steinberg	2	1	autocovariability or cross-covariability	interaction
II	Altmann	4	3	cross-covariability	autocovariability, interaction
III	Marko-Neuburger	4 (6..)	1 (2..)	analogues of cross-covariability	first-order transmissions
IV	Van den Bercken-Cools	3	1	autocovariability cross-covariability interaction	

such a combination can not only consist of sequentially ordered variables (such as for instance, I_{t-1}, I_{t-2} and I_{t-3} in Altmann's model), but also of simultaneously occurring variables (such as I_{t-1} and J_{t-1} in our model) and even of a mixture (e.g. I_{t-1}, I_{t-2}....J_{t-1}, J_{t-2}....K_{t-1}, K_{t-2} etc.). In fact, the most complete set of factors that can determine I_t, consists of all the preceding behaviours of all individuals. This is clearly an extreme case. The question then arises as to the criteria for identifying a special subset of predictors, i.e. for a structural model of the dependent variable. The rationale for an information-statistical model of interaction sequences was originally based on the fact that information theory was devised for studying the properties of information sources and communication channels. In fact, some early ethological applications of the theory intended apparently not only merely to adapt its statistical basis to animal behaviour but also to imply some real analogy between animal behaviour and technological communication systems (see references in Hazlett and Bossert, 1965; cf. Altmann's Markovian signal source and Marko's stochastic automata; see also Moles, 1963 and Kalmus, 1969). The mere fact, however, that information-statistics may be used to describe certain aspects of animal behaviour need not imply that technological communication systems provide an appropriate model for animal communication. At present, information statistics is mainly considered as a useful formalism for the analysis of certain relationships in interaction sequences, but the relationships of interest remain for the most part those considered to represent communication. The latter is even defined as a significant correlation between subsequent behaviours (Wilson, 1975). But then again, in observed interaction sequences there are many candidates for such correlations, as pointed out above: how can the correct ones be selected? We believe that the best strategy is to focus on first-order transitions for pairs of individuals and to avoid confusing communication between individuals with intra-individual sequential contingencies. It is admittedly not very difficult, especially in the context of primate social behaviour, to find instances of higher-order sequential effects in

a behaviour sequence. For example, "approach" combined with "open-mouth threat" result most frequently in "flee", while "standing" and "open-mouth threat" mostly result in submissive expressions such as "bared-teeth grin" and "lip-smacking". Higher order effects of simultaneous behaviours of several individuals are also easily found. In fact, many of the more interesting interactions in macaques involve a number of individuals and a number of consecutive behaviours (De Waal et al., 1976). Nevertheless, as long as most communication in a group involves only two subjects and first-order transitions, an analysis-of-variance will be able to represent it sufficiently; all remaining effects together with noise will come under the label of residual variability. This argument already touches upon the next problem to be discussed: that of the scope of an information-statistical model as such.

Scope of information-statistical models

It should be realized that any statistical model is global and abstract with respect to the single, concrete behavioural items making up a behaviour sequence. It does not allow for statements on the formal properties of any behaviour or on the meaning of individual elements, since it represents average effects and therefore global properties of the behaving system. This indifference for particular behaviours is also an advantage. The approach of identifying communication by correlations between consecutive behaviours has the virtue of avoiding a commitment to what are fundamental difficulties. For instance, the problem of explicitly identifying and defining communicative acts as a proper subset of behaviour is avoided, since "any behaviour pattern whose occurrence changes the probability of other behavioural patterns will be regarded as a communicative act" (Altmann, 1965). Furthermore, by using probabilities of occurrence of behavioural acts we are not obliged to describe whether certain behaviour patterns or acts are communicative in an all-or-none fashion, or whether all behaviour, by being observable, is communicative in some degree, from "not at all" to "completely". It is of course possible to determine for each separate

behaviour a response variability, based on the distribution of following acts, and then to rank the behaviours as more or less "communicative". This does not however solve the latter problem. Suppose we find for a certain behaviour X a response variability of 60% (the scale ranging from zero variability to a maximal variability, or 100% for random conditions). In such a case we do not know whether X fully determines the response in 60% of the combinations involving the preceding behaviour or whether X partially determines the response by an amount averaging 60% in all the combinations. Should these difficulties be considered to encompass relevant problems, other approaches must be tried for their solution.

The main usefulness of information-statistical models lies in the fact that they yield statistical indices. First of all, if one accepts that such factors as autocovariability and cross-covariability (or communication) are important in the organization of ongoing behaviour, an analysis-of-variance enables the detection of the actual presence of these factors and the establishment of their magnitude. The model as formulated in equation (8) generates specific predictions such as the following: a) an individual's current behaviour is significantly dependent on his preceding behaviour, i.e. the autocovariability is larger than zero; b) an individual's current behaviour depends on his partner's preceding behaviour, i.e. the cross-covariability will be significantly larger than zero; c) both factors are presumably sufficient for explaining the total individual variability: the total sequential covariability does not significantly differ from the total variability. It should however be kept in mind that a statistical model always fits the data when it is not constrained by limiting the parameter space. Statistics describe the stochastical structure of an empirical system; a statistical model is never a theory of behaviour unless it is constrained.

Secondly, the possibility of quantifying these factors is especially useful in ethological studies on social behaviour. This issue is discussed in chapter 7.

CHAPTER 6

EMPIRICAL COMPARISON OF INFORMATION-STATISTICAL MODELS OF INTERACTION SEQUENCES

The attempt to measure communication in ethology has resulted in several information-statistical models characterizing the relationships between individuals as observed in interaction sequences. The common assumption is that communication between individuals is reflected in correlation between their ongoing behaviour. In chapter 5 it was shown that the models differ in the identification of the relevant correlations and in the way these serve the purpose of measuring communication. In chapter 4 we presented a general model for separately measuring the effects of two simultaneous constraints on the ongoing behaviour of an individual in a social situation: inter-individual constraints (= "communication") as manifest in correlations between the current behaviour of a reference subject and the preceding behaviour of another subject, and intra-individual constraints, appearing in correlation between the current and preceding behaviour of the reference subject. In this chapter we present an empirical comparison of this model with several others as applied to data derived from observation of social interaction in Java monkeys. The four models are summarized in Fig. 6.1.

I. In the first model, communication between two individuals i and j is primarily apparent from first-order inter-individual sequential dependencies; the current behaviour of one individual is a function of the preceding behaviour of the other.

II. Here, sequential dependencies in interaction sequences represent communication; the current behaviour of i is a function of at least three preceding behaviours in other individuals.

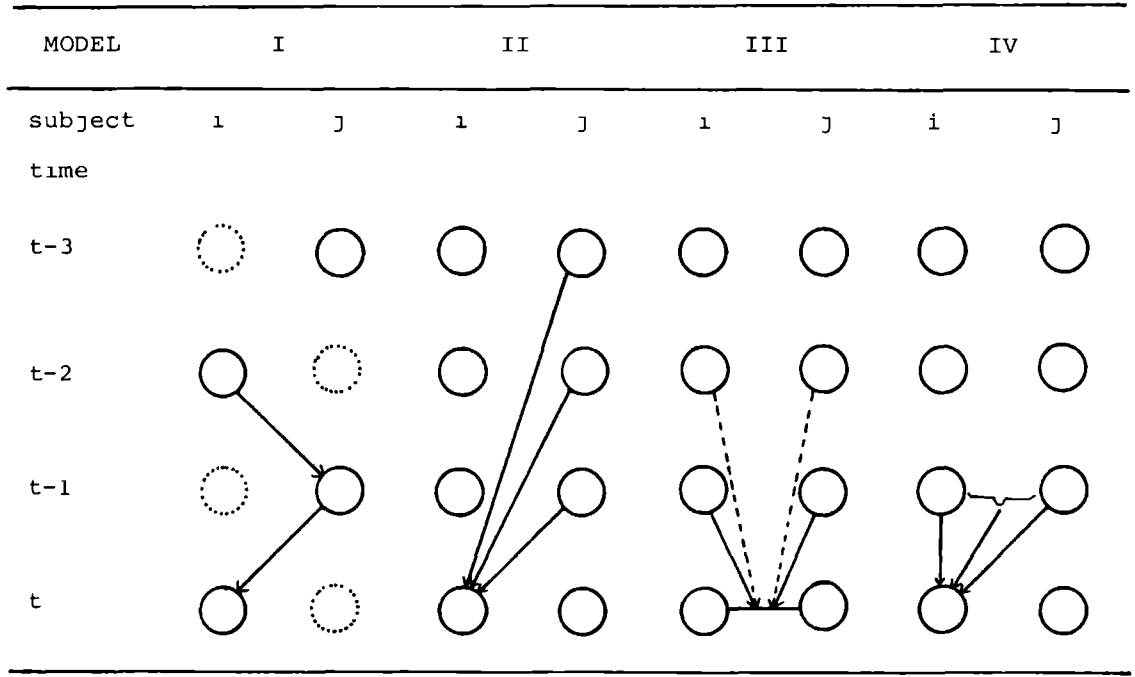


Fig. 6.1

Schematic representation of a number of models of social interaction and communication. Columns headed by i and j are behaviour sequences of i and j respectively (indexed by t). Arrows indicate presumed causal relationships between behaviours. Open circles indicate dummy states, by which sequences are made properly alternating.

III. In the third model correlation between simultaneously occurring behaviours is a consequence of communication between i and j; this correlation is a function of the preceding behaviours of both i and j.

IV. The fourth model treats sequential constraints in interaction sequences as due to communication; the current behaviour of i is a function of both i's and j's immediately preceding behaviour; the separate effects of these behaviours on the current behaviour of the reference subject i are measured by partial auto- and cross-covariability.

The structure of models I-IV and their information-statistical formulation have been fully discussed in chapters 4 and 5. Every model can be regarded as explaining the variability of the ongoing behaviour of the individual under study (the reference subject) by relating it to the variability of preceding behaviour. The degree of inadequacy in this explanation is reflected in a term of "residual variability", and the amount of residual variability is an index of the relative success of a model in identifying the relevant sources contributing to the variability of ongoing behaviour. We will compare models I-IV in respect of their residual variability by applying them to the same set of data.

SUBJECTS AND EXPERIMENTAL DESIGN

Data for the analysis of social interaction were collected from observations of Java-monkeys imported from the Philippine Islands. Six different triads were put together from five adult monkeys, two males (Ka, 4.6 kg; and Bo, 5.4 kg) and three females (El, 3.5 kg; Sa, 3.9 kg; and Be, 3.7 kg), always consisting of one male and two females. The composition of the triads is shown in Table 6.1.

The study of social interaction was part of a neuro-ethological research project on the role of certain neostriatal transmitters in the determination of ongoing behaviour (see chapters 9-11). The data reported upon in this chapter were based on observations made in the control conditions, i.e. when the mon-

TABLE 6.1

Composition of triads, and reference subject in each triad (1 = Ka, 2 = Bo, 3 = El, 4 = Sa, 5 = Be)

triad nr	monkeys in triad					reference subject	number of hours of observation
	m	m	f	f	f		
1	1		3	4		1	5
2	1		3		5	1	5
3		2	3	4		2	4
4		2	3		5	2	5
5	1		3	4		4	5
6		2	3	4		4	5

keys had received small injections of aqua destillata into the caudate nucleus.

Throughout the experiments the monkeys were housed in a cage of dimensions 2 x 3 x 2 m, under relatively constant conditions of temperature and humidity. The cage was placed inside a Faraday cabin. It had a sash window in the middle of one of the shorter sides and a fixed window in the right upper corner of the same side. One long side and part of the ceiling were equipped with climbing grids. There were two transverse perches, a swing hanging from the ceiling and three small benches fixed on the other long side. The upper half of the side opposite the sash window was divided into four compartments by means of horizontal perches and vertical partitions. The monkeys had free access to food and water (consisting of ordinary laboratory pellets and fruit, delivered twice daily at 8.00 a.m. and 5.00 p.m.). The cage was cleaned twice a week; in other respects the monkeys were not disturbed during the experiments. There was an artificial day-night cycle with day-time simulated from about

7.45 a.m. to 6.30 p.m.; the onset of day-time was gradual, taking about half an hour.

The behaviour and social interactions of the monkeys were observed and protocolled in a series of daily sessions lasting one hour, always in the period 8.30 to 10.30 a.m. Injections were always given at the beginning of a session.

THE RECORDING AND PROTOCOLLING OF BEHAVIOUR

The behaviour of the monkeys was observed, recorded and protocolled by the method outlined in chapter 3. The ethogram used for identifying and coding their behaviour has been described in chapter 2. As the number of elements in the state set is related to the number of observations needed to endorse statements concerning properties of that state set (e.g. its variability), a convenient size of the ethogram is advantageous. Our original ethogram consisted of 95 elements, mostly identified from the available literature; a few were added during actual observation of the monkeys. This number is rather high, allowing $95^2 = 9025$ first-order combinations and $95^3 = 857\,375$ third-order combinations, and consequently required samples of considerable size. The variability measure is a sum of terms $p.\log_2 1/p$ (where $0 \leqslant p \leqslant 1$). It can be seen from this function that low-probability occurrences contribute relatively little to the measure of observed variability; in addition small variations in probability have little effect (for examples, see Quastler, 1955). We decided therefore to use a subset of the ethogram, consisting of the items that accounted for at least 85% of the observation time. This resulted in 49 different behaviours. A list of the items is to be found in the Appendix to this chapter.

Protocols were made from the videotapes by registering the behaviour of the monkeys as follows. At the beginning of each session the initial state description of each subject was entered, consisting of codes for behaviour, location, and orientation towards partners or objects. During the session only changes in this state were entered; the codes which remained appropriate for individuals in unchanged state were

inserted in the protocol by the processor. It should be noted that the time base of the protocol was fixed by recording anew the ongoing behaviour of each individual whenever at least one changed his behaviour. In this way, the same behaviour may repeatedly occur in one subject by virtue of the fact that another individual has changed his behaviour. Although the duration of each behavioural occurrence may vary, only occurrences of behavioural states are considered in the present study, irrespective of their duration. The resulting protocols consisted of a time-series of group state descriptions or, equivalently, a set of simultaneous individual time-series, obtained from continuous observation over a period of one hour per experiment session. All the protocols obtained from observations where the experimental conditions were identical, were concatenated for the analysis.

ANALYSIS OF THE DATA

Data appertaining to the three reference subjects in the six triads were used. With each reference subject the remaining two individuals in the triad were pooled into one "other" or partner by the following procedure. Firstly the dyadic combination of the reference subject and one of the others was taken; then the combination of the reference subject and the third subject was added; and finally the model parameters were computed. The procedure may be illustrated by reference to Table 6.1. The five protocols resulting from observing the first triad, consisting of subjects Ka, El and Sa, were concatenated into one protocol. The relevant behaviour combinations were listed in turn for pair Ka and El and for pair Ka and Sa. As Ka was taken as the reference subject, the relevant combination of events consisted of the current behaviour of Ka, the preceding behaviour of Ka and the preceding behaviour of El and Sa in turn. In all six triads monkeys Ka, Bo and Sa all occurred four times as reference subjects; El figured six times as partner, Sa and Be twice and Bo and Ka just once.

The relevant combination of events (current behaviour of the reference subject, I_t, and preceding behaviour of the reference

subject and his two partners, I_{t-1}, J_{t-1} and K_{t-1}) was only considered appropriate for further analysis if each of its behaviours was an element of the above mentioned restricted ethogram. It was counted as follows. First the combinations I_t, I_{t-1} and J_{t-1} were extracted from the protocol and then the combinations I_t, I_{t-1} and K_{t-1} were added.

RESULTS

The results of fitting models I-IV to the data are presented in Table 6.2. The sample size is the total number of combinations of behaviour of the reference subject and one partner (the actual number of behavioural state descriptions in the protocols is only half this, as each observation of the behaviour of the three subjects in a triad provides two dyadic combinations). The total individual variability of the ongoing behaviour of each reference subject is represented by the usual informational statistic describing the distribution of the frequencies of each behaviour. The maximum variability associated with a repertoire size of 49 elements is 5.61 bits (= 100%). The residual variability is the amount of individual variability that cannot be related to or explained by any of the factors supposed to influence ongoing behaviour. In model I the residual variability is 58%. Consequently, 100% - 58% = 42% of the total individual variability can be accounted for by first-order inter-individual influences or "communication". Taking the effect of three preceding behaviours for communication as in model II, results in a residual variability of 41%, "communication" now accounting for 59% of the total individual variability. Identifying communication with correlation between simultaneous ongoing behaviour (model III) leaves 72% of the criterion variability unexplained: only 28% can be related to communication. When autocovariability effects are also considered (model IV) the residual variability is reduced to 23%. The decrease in residual variability in models I, II and IV is a consequence of the fact that additional predictors are involved in models II and IV. The cross-covariability value for first-order inter-individual transitions is the same in models I, II and IV.

TABLE 6.2

Total individual variability in the ongoing behaviour of reference subjects from different triads and with different residual variability, i.e. the amount of individual variability not accounted for by factors hypothesised in the various models to be related to social interaction and communication

reference subject	sample size	individual variability (in bits)	residual variability in model*			
			I	II	III	IV
Ka	2864	4.10	69	59	82	32
Ka	2604	4.28	73	48	76	28
Bo	2914	4.27	64	39	83	27
Bo	2826	4.04	52	48	79	24
Sa	2436	3.79	46	29	55	14
Sa	2776	3.94	42	23	57	13
		Mean	58	41	72	23
		Range	42-73	23-59	55-83	13-32

* *as proportion (%) of individual variability*

DISCUSSION

From the point of view of individual variability, model III seems to be the least successful: 55% to 83% remains unexplained in the various triads, with an average of 72%. As far as communication is concerned this suggests that about 28% of a monkey's ongoing behaviour is correlated with the ongoing behaviour of other monkeys. In the limiting case, this amount is determined exclusively by the preceding behaviour of others; then 28% of the variability in the reference subject is due to communication. Now it can be seen from the average residual variability of model I that first-order inter-individual covariability accounts for 100% - 58% = 42% of the reference variability. In the limiting case, again, there is no interaction; meaning that all of the cross-covariability, 42%, represents communication. This implies that model I is better for measuring communication. Therefore, interpreting first-order inter-individual transmission as representing communicative effects appears to be not only more direct but also more effective.

The foregoing reasoning is based on the limiting cases of models III and I respectively, resulting in the maximum amount of communication that each model can recover. It should be noted, however, that although the consequences of the limiting cases of models III and I are the same, the actual conditions generating the limiting cases are different. When in model III correlation between concurrently occurring behaviours of i and j represents only effects due to j (communication from j to i) this implies that there is no communication from i to j. When in model I the cross-covariability represents only communication this implies that there is no interaction covariability for i. Model III is much more rigorous than model I, in that the actual value for communication from i to j sets a limit on the communication from j to i. The value of the cross-covariability between i and j in model I has no effect on the cross-covariability between j and i. Whatever the probability of each condition may be, it is clear that with respect to measuring communication each model has its own maximum under the limiting conditions.

Independent of the occurrence of the limiting case is the possibility that the parts of the correlation between the co-occurring behaviours of i and j in model III are proportional to the cross-covariabilities in model I (or to the partial cross-covariabilities in model IV). Even then, model III can be considered to be less efficient, as it accounts for a smaller part of the absolute amount of communication present in the interaction sequence and thereby leaves more of it in the residual variability. Therefore, a comparison of models III and I turns out in model's I favour, in respect of both the total individual variability explained and the amount of communication recovered.

Model I is however optimal only in the limiting case where interaction covariability is absent. As it does not make provision for the possibility of that effect, the cross-covariability of 42% found in model I, need not actually be identical with communication. We have to separate the cross-covariability from the interaction covariability, as is done in model IV. For the data in Table 6.2 only the residual variabilities were computed, and to appreciate the consequences of confusing auto- and cross-covariability the reader is referred to Table 7.2, where separate covariability terms are given according to model IV. Two types of interaction terms are found: a positive one, representing the effect of either one of the predictors, and a negative one, representing the effect of both predictors together. The original cross-covariability term overestimates the effect of communication, especially in the case of a positive interaction term. For instance, in subject Je, the partial cross-covariability of 0.80 and the interaction covariability of 0.34 make up the original cross-covariability or inter-individual transmission of 1.14, implying that about 30% of the latter is not solely due to inter-individual effects.

From the data in Table 6.2 it can be seen that a consideration of second- and third-order inter-individual transitions as well (model II) is more effective than of first-order transitions alone (model I): the residual variability is reduced on average from 58% in model I to 41% in model II. However, the degree of confounding the effects due both to the preceding behaviour of

the reference subject itself and to the preceding behaviours of others is much more serious in model II than in model I. Model II neglects that part of the total individual variability that can be accounted for by autocovariability and in addition identifies communication with transmissions that do not exclusively represent inter-individual effects. Taking more account of the preceding behaviours of others does indeed, therefore, improve the predictability of the current behaviour of the reference subject but at the same time confuses the sources of this improvement: it is certainly not communication alone that is responsible.

If we keep to first-order transitions, as in model I, but also allow intra-individual effects (autocovariability), as in model IV, the residual variability is reduced to only 23%. This means that it is not merely an increase in the number of predictors (model II vs model I), but rather the selection of the right predicting variables (model IV vs model II) that is effective in explaining individual variability. To sum up: with respect to individual variability, the order of effectiveness for the models is III - II - I - IV. With respect to communication (defined as exclusively inter-individual effects) the order becomes III - I - II - IV. The reversal of I and II is a consequence of the fact that there is much better identification of effects in model I than in model II.

An additional comment must be made regarding model II, which was used by Altmann (1965) in a study of communication in rhesus monkeys. Up to this point we have discussed it only in comparison with other models when applied to our data. In Altmann's original work Markovian models appear to be much more succesful: a third-order model fitted his data almost perfectly, leaving a residual variability of about 12%. It does not however seem appropriate to be very concerned about this difference in outcome as there are obviously differences in both methodology and procedure. Although further research is needed to identify the conditions favouring the prevalence of third-order inter-individual constraints or of first-order inter- and intra-individual constraints in behaviour sequences, the following comments may be made.

Altmann reports an average individual variability of 4.80 bits; this is somewhat higher than our values, which range from 3.79 to 4.28 bits (Table 6.2). This may very well be due to the fact that our triads represent relatively simple communities as compared with larger groups of monkeys. (Note: the individual variability of monkeys in a group of six members turned out to be somewhat higher than that of the monkeys in the triads - compare Table 7.2.) After first-order cross-covariability effects in Altmann's data have been accounted for, a residual variability of 60% is left (Altmann, 1965), which is remarkably close to the mean of 58% in our data (Table 6.2). However, our residual term after analysis of third-order inter-individual effects is 41%, more than three times as high as Altmann's 12%. We considered the possibility that our sample sizes, ranging from 2,436 to 2,914 are inadequate compared to Altmann's 5,507 for detecting higher order effects. We therefore checked this by combining all the protocols from all the triads into one protocol, giving a sample size of 16,424. Further application of Altmann's model yielded a residual variability of 32%; a definite improvement on the original value of 41%. When we applied our own model as well to this set of pooled data we found a residual variability of 19%. As a result of enlarging the sample, therefore, the original difference between model II and model IV was reduced from 18% (41% - 23%) to 13% (32% - 19%). Sample size does therefore affect the goodness of fit of a model *per se*, but does not seem to affect the relative efficiency of models.

Finally, another possibility may exist to explain the goodness of fit of the Markov model in Altmann's study. From Altmann's report it appears that he included interaction sequences only when generated by individuals that were at the same time both fully observable and obviously interacting with each other. The number of interactants was usually quite small, "generally consisting of two or three monkeys at a time". Moreover, some (or all) of the acts preceding the current behaviour of the reference monkey could be performed by the same or by different partners. It seems also to have been possible that the preceding behaviour was of the reference monkey itself. "An event was counted regardless of

whether or not previous actions were performed by the same monkey". Altmann sampled sequences composed therefore of transitions produced by a few individuals actually interacting. Our data in Table 6.2, on the other hand, consists of all the observable transitions produced by three individuals, not just those manifesting actual interaction.

However, part of the data in Table 7.1 seems to be of the same nature as Altmann's data. The first column presents covariability parameters for explicit (actual) interaction (including only transitions of interactants which were observably oriented at each other). In this case we found a total individual variability of 4.14 bits and a first-order intersequential covariability of 3.12 - (.20 * 3.12) /4.14 = 60%. First-order cross-covariability in Altmann's data was 40%. This implies that our criteria for identifying explicit interaction appear to have been more stringent.

APPENDIX: BEHAVIOURAL ITEMS

Items	Comment
sitting alert	and looking round
sitting hunched	head and shoulders bent down
standing	on all fours
standing up	on hindlegs
lying on side	
lying on back	
walking	on two, three or four legs
climbing	
brachiating	
jumping	
shaking	head, or head and shoulders
scratching quickly	reflex-like activity
scratching slowly	attentively
grooming-self	including cleaning of wounds
yawning	
looking at	directed eye movements
sniffing at	bringing nose close to an object
licking at	
eating	including picking up and cleaning food
drinking	irrespective of morphology
slapping	on ground or perch
fixating	("frowning" and) staring intensively at
averting the gaze	avoiding looking at
flattening ears	and holding them flattened
scalp retraction	
bared teeth grin	retracting upper (and lower) lips
open mouth	threat
open mouth grin	bared teeth + open mouth
lip smacking	including repeatedly protruding the tongue
head bob	thrusting the head forward without locomotion
shoulder bob	
lunging	moving forelegs only
shrinking	backwards without locomotion
crouching	pressing the body to the ground
presenting	sexually
inviting	for grooming
moaning	soft, humming-like
grunting	
continuous grunting	repeatedly and loudly
screaming	high-pitched
running after	chasing around
running away	fast locomotion away from other
following	moving along behind another
touching	putting hand on another
grooming	another monkey
being groomed	
inspecting	especially anogenital checking
mounting	
copulating	pelvic thrusts

grasping	and holding
pulling	violently
pushing away	
striking at	without actually hitting
play-wrestling	
huddling	head resting on other

General comment

Whenever two items occurred simultaneously, the item with the lowest position in the list was recorded, e.g. "fixating" + "grunting" = "grunting". When two such items had different orientations towards object or partner, it was sometimes possible to take one item as reflecting the orientation of the other, e.g. "eating" + "looking at A" = "eating, oriented towards A". When this solution was not possible, the item and orientation considered most important were scored, e.g. "presenting for A" and "fixating B" becomes either "presenting for A" or "fixating B", depending on the circumstances. When a monkey's behaviour was not observable (because another monkey is between the former monkey and the camera) the item "not observable" was recorded. In the analysis of the data this item was treated as if it were a behavioural state.
(Note: this list includes some additional items, used in the next chapter.)

CHAPTER 7

ASPECTS OF COMMUNICATION AND GROUP STRUCTURE IN JAVA MONKEYS

Although the data-analytical procedure developed in chapter 4 was primarily intended for the identification and quantification of two kinds of constraint acting on ongoing behaviour, it appeared to offer possibilities for further application, in particular in the analysis of formal aspects of communication and of dominance relationships. This chapter shows how certain aspects of our intuitive or common sense notions of communication can be measured in animal behaviour by applying a formal model to observed data, or, equivalently, how quantitative relationships observed in particular collections of data can be interpreted as reflecting communicative processes or even "personality traits".

FORMAL ASPECTS OF COMMUNICATION

Identifying changes in the probability of behaviour with communication does not preclude the need for further explanatory hypotheses. We attempted therefore to relate the measurement of inter- and intra-individual constraints to a proposal for a formal analysis of communication. Mackay (1972) distinguished several types of (non-verbal) communication, according to the presence or absence of goal directness ("intention") in the actor and the interpretation of it in the recipient. We decided to investigate how the relative weight of inter- and intra-individual influences on the variability of a monkey's current behaviour varies according to the type of interaction, i.e. according whether "intention" is involved or not. Overt orientation towards another monkey was taken as evidence of the presence of an intention to communicate

or of its perception. Behaviourally, signs of intention include: physical contact, locomotion and gestures towards another individual; and gaze, facial expressions and vocalizations directed at another, identified, subject.

Experimental methods

For the analysis of responsiveness under various conditions of orientation, the same data were used as in chapter 6, but, this time the three reference subjects were pooled. The dataset was made up as follows. Firstly, all the protocols were concatenated into one protocol, after which the relevant combinations of events were sorted into four lists according to the orientation of the interactants, corresponding to the following orientation conditions: (I) mutual orientation when both the reference subject and his partner were showing behavioural signs of orientation towards one another; (II) only partner oriented at reference subject; (III) only reference subject oriented at partner; (IV) no mutual orientation. The relevant combinations of events consisted of the behaviour of a reference subject (Ka, Bo or Sa), the preceding behaviour of the reference subject, and the preceding behaviour of the partner (each of the remaining monkeys in the triad in turn).

Results

The variability components characterizing the interaction between reference subject and partner under different conditions of orientation are summarized in Table 7.1. The total individual variability is again the usual H-measure of the frequency distribution of behaviour. The total sequential covariability is the total amount of variability in the current behaviour of the reference subject that can be accounted for by the preceding behaviour of the reference subject itself and the preceding behaviour of his partner. The partial covariabilities are expressed as proportions of the total sequential covariability. The values of the auto- and cross-covariability were compared for conditions I against II and III against IV by means of the testing procedure described in chapter 8. The covariabilities in condition II differ sig-

TABLE 7.1

Components of the variability in the current behaviour of the reference subject under different conditions of orientation

Orientation conditions	I		II		III		IV	
reference subject partner	R	P	R	P	R	P	R	P
preceding behaviour	←		←					
subsequent behaviour	→				→			
sample size	2955		2517		2407		8541	
H_1	4.14		4.26		4.37		3.95	
$T_{1:1j}$	3.12		2.84		2.97		2.78	
a_{1j}	20%		39%*		34%		48%**	
c_{1j}	59%		47%*		55%		44%**	

H_i = *total individual variability*
$T_{i:ij}$ = *total sequential covariability*
a_{ij} = *partial autocovariability (proportion of* $T_{i:ij}$*)*
c_{ij} = *partial cross-covariability (proportion of* $T_{i:ij}$*)*
Arrows indicate the direction of orientation

* = *difference between I and II has* $p < .01$
** = *difference between III and IV has* $p < .01$
according to statistical procedure in chapter 3.

nificantly from those in condition I, and the covariabilities in condition IV differ significantly from those in condition III.

Discussion

The results on the role of orientation reflect some interesting characteristics of social interaction in monkeys. For instance, even when monkeys in small groups (triads) do not specifically show behavioural orientation towards one another, their behaviour appears to be subject to some form of reciprocal constraint. In condition IV (no mutual orientation) 44% of the total sequential covariability in the reference subject can be accounted for by

the previous behaviour of the partner. Several explanations are possible of the presence of inter-individual effects in the absence of mutual orientation. Absence of externally observable orientation in the monkeys can apparently not be equated with absence of intention or absence of perception of intention. Firstly, a human observer may be unable to detect all relevant cues because of intrinsic limitations. Secondly, direct behavioural orientation, especially in a small group, need not be the only form of reciprocal constraint. For instance, chemical communication or seemingly undirected vocalizations may play a role. Finally, external factors identical for all members in a group may have a synchronizing effect on their ongoing behaviour. Whatever the case may be, the cross-covariability of 44% for the condition of no mutual orientation may be considered as a kind of base-line "tuning-in" to each other. When the monkeys interact explicitly, as in condition I, the cross-covariability is 59%. This value can be interpreted as a sort of upper limit, sufficient for stable relationships in a group, at least in the present experiment.

The relevance of these data does not lie solely in the fact that they confirm the truism that the presence of orientation affects behaviour. Rather the data are of interest because they show how much difference orientation can bring about, expressed according to the relative weights of intra- and inter-individual influences on behaviour. Alternatively, the attempt to quantify the effects of "intention" as operationalized in "orientation" can be regarded as essentially valid, as the categories into which the observations were sorted, were not filled at random. The criteria for classification appear to represent real properties of the data and consequently of the monkeys.

FACTORS DETERMINING DOMINANCE RELATIONSHIPS

The term dominance is used for describing relationships between individuals (i is dominant over j) and for characterizing groups (a group has a dominance structure or hierarchy). A relationship is supposed to exist between both applications:

the dominance hierarchy should reflect inter-individual behavioural interactions. "Dominance" is also used as an explanatory concept: a hypothetical internal state or an intervening variable (Deag, 1977), accounting for the observed relationships between individuals, again used at the individual level (as an attributed personality trait) and at the social level (as an "emerging property" of a group). In both cases it is very difficult to demarcate the domain of observed behaviour from which the concept is inferred and the domain of behavioural characteristics to be explained by the concept.

Whatever the case may be, the notion of dominance implies an ordering of individuals with respect to some characteristic, e.g. being limited by the behaviour of others (Deag, 1977), or having influence on them. Estimates of covariability provide an obvious set of measures for such a ranking. The relationship between the preceding and subsequent behaviours of two interactants, i and j, is characterized by four parameters (Fig. 7.1): the partial autocovariabilities a_{ij} and a_{ji}, and the partial cross-covariabilities c_{ij} and c_{ji}. These parameters can be interpreted as individual characteristics or personality traits determining the dominance relationship between i and j. Individual i is said, for instance, to be dominant over individual j, if i has more control over j's behaviour than j himself has: formally, when $c_{ji} > a_{ji}$; or, alternatively, i is considered dominant with respect to j, if i has more influence on j's behaviour than j has on i's: formally, when $c_{ji} > c_{ij}$. Again, i is dominant over j, if he is more autonomous than j: when $a_{ij} > a_{ji}$. The terms a_{ij} and c_{ij} may or may not be empirically correlated. When they are not correlated, dominance relationships between i and j can be expressed by combining both terms, e.g. i is dominant over j when $a_{ij}/c_{ij} > a_{ji}/c_{ji}$. This would imply that "autonomy" and "control" are independent factors in determining dominance relationships between individuals.

Experimental methods

The data for the analysis of dominance relationships were collected from observations of a small group of six Java-monkeys (Macaca fascicularis), which had been individually imported from

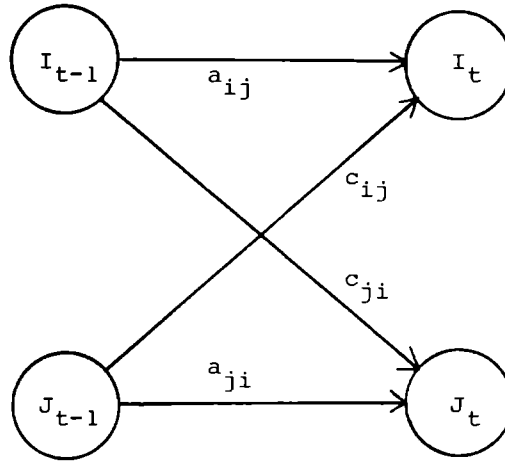


Fig. 7.1

Directed graph of the relationships between the preceding and subsequent behaviours of a reference subject i and his partner j. Labels by the arrows denote covariabilities which make up part of the variability in the current behaviours (I_t and J_t), and reflect presumed causal influences from the preceding behaviours (I_{t-1} and J_{t-1}).

the Philippine Islands and housed in a communal cage for nine months before the observations started; after this time the group structure could be considered stable. The group consisted of two adult males (Je, 6.2 kg, and Pi, 4.8 kg), one adolescent male (Ja, 3.5 kg), and three adult females (Tu, 3.9 kg, Ne, 3.3 kg, and Mi, 3.8 kg). The observations of the group took place between 8.30 and 10.30 a.m. in observation sessions lasting one hour.

The methodology for observing and protocolling behaviour is described in chapter 3. The data were derived from 26 hours of observation. A subset of the original ethogram, comprising 85% of the total number of observed behaviour frequencies was used. This subset consisted of 56 items and is listed in the appendix of chapter 6.

As it is virtually impossible to obtain a detailed, continuous and simultaneous description of the behaviour of all the individuals in a group of six, even with two cameras at hand, we used the following method of observation. Each animal in the group was taken as reference subject for at least four observation sessions. His own behaviour and the behaviour of the subjects with which he was interacting were recorded, but the behaviour of the subjects that were not directly interacting with the reference subject was not protocolled. The reference subject was considered to be interacting with other monkeys when his behaviour was observably oriented towards another subject, or when another subject observably directed his behaviour towards the reference subject, or when both situations existed. "Orientation" was once again defined to be present when physical contact occurred or when gaze, gestures or locomotion were directed at an identifiable partner. The protocols for each individual i in the group were concatenated and analysed as representing dyadic interaction between the subject i and a generalized partner j, where j could actually be any of the five other individuals in the group. Although five of the six monkeys were equipped with a device for chemical telestimulation, the observations for this analysis were made in "control conditions", without injections. The parameters supposedly determining dominance relationships were computed for each individual i, and in order to evaluate the usefulness of covariability parameters for assessing dominance relationships in a group, one of the conventional indices for dominance was also computed: the ratio of the number of threats made to the number received. "Threat" was defined to apply when a monkey showed the facial expression "staring open mouth face" (Van Hooff, 1967; Angst, 1974).

Results

The parameters characterizing inter-individual relationships in this group of six monkeys are summarized in Table 7.2. The covariability terms a_{ij} and c_{ji} are to be regarded as absolute attributes of subject i, consequent upon our sampling procedure. For each reference subject i the parameters a_{ij} and c_{ij} were

TABLE 7.2

Covariability parameters as determinants of group structure

reference subject	sample size	H_i	$T_{i:ij}$	a_{ij}	c_{ij}	x_{ij}	$\frac{a_{ij}}{c_{ij}}$	number of threats made/received
m Jc	1157	4.55	3.09 68%	1.95 63%	0.80 26%	0.34 11%	2.42	$\frac{33}{3}$ = 11.00
f Mi	1294	3.81	2.42 64%	1.45 60%	0.80 33%	0.17 07%	1.82	$\frac{34}{29}$ = 1.17
f Tu	1265	4.04	2.71 67%	1.85 68%	1.20 44%	-0.33 - 12%	1.54	$\frac{20}{8}$ = 2.50
f Ne	1174	4.66	2.84 61%	1.36 48%	1.11 39%	0.37 13%	1.23	$\frac{17}{18}$ = 0.94
m Pi	1341	4.15	3.02 73%	1.66 55%	1.63 54%	-0.27 - 09%	1.02	$\frac{16}{25}$ = 0.64
m Ja	980	4.59	2.84 62%	1.65 58%	1.87 66%	-0.68 - 24%	0.88	$\frac{9}{46}$ = 0.20

H_i = total individual variability; $T_{i:ij}$ = total sequential covariability; a_{ij} = partial autocovariability; c_{ij} = partial cross-covariability; x_{ij} = interaction covariability

For each subject the first row gives the absolute values in bits and the second row percentages ($T_{i:ij}$ in relation to H_i, and the partial covariabilities in relation to $T_{i:ij}$).

computed from data in which j could be "anyone else" in the group. The autocovariability of i given j is therefore an index of the autonomy of i with respect to a "generalized other". The cross-covariability of i given j similarly means the amount of control exerted on i by other individuals in general. The rank orders based on the parameters in Table 7.2 are as follows. For "autonomy", as measured by partial autocovariability, we have: Je-Mi-Tu-Ne-Pi-Ja. For "experienced control" the order is: Je-Tu-Mi-Ne-Ja-Pi. Combining a_{ij} and c_{ij} gives: Je-Mi-Tu-Ne-Pi-Ja, while finally, from the number of threats, we get: Je-Tu-Mi-Ne-Pi-Ja.

Discussion

The dissimilarity in rank-order resulting from the different parameters presented in Table 7.2 is not very great. A dominance hierarchy to account almost perfectly for all the observed rankings would be: Je-(Tu/Mi)-Ne-Pi-Ja. This precisely because there is so much agreement, that difficulties arise in evaluating the differences. Nevertheless, some general comments can be made. Two strategies are possible for constructing a dominance hierarchy: 1) the characterization of each dyadic relationship by a dominance measure followed by the derivation of an overall ranking of the individuals in the group; 2) a direct characterization of each subject by some relevant property with a ranking to suit. In the first case, for a group of n subjects, ½n(n-1) parameters are needed while the latter approach, which was used in the present study, needs only n parameters. The number and the nature of the characteristics to be measured may also vary. One may use global characteristics such as our auto- and cross-covariabilities based on observations of long sequences of interaction and the use of all the information in them, or specific characteristics such as particular behaviours, for instance threat signals or the frequency of mating. The number of parameters also depends on the number of measured characteristics. Two problems can arise: measurements of a single characteristic do not yield an unidimensional ranking, and multiple measurements cannot be reduced to an unidimensional scale. The latter problem occurs when rank-orders

based on different tests do not correlate with each other. In both cases several factors appear to be necessary for the establishment of a dominance hierarchy. An overall characteristic of individuals based on observing all kinds of behaviour can be attractive, because it does not capitalize on isolated facts. The choice between relational characteristics (for pairs of subjects) and individual characteristics depends again on theoretical considerations: is dominance a consequence of some personality trait, an absolute attribute of an individual (such as body weight for instance) or not? To conclude: the discussion on the extent and the validity of the concept of dominance is not by itself advanced by using the kind of measures developed in the present chapter. However, given the context of this discussion, it may be of some help that informational statistics can be used to quantify certain properties of an individual and its relationships with others.

GENERAL DISCUSSION

When applying a statistical model to an interaction sequence, specific relationships between particular behaviours are obscured. In particular, the semantic content (what an animal does) is not taken into account; agonistic and friendly interactions, for instance, contribute to cross-covariability in the same way. Our aim was to detect and measure intra- and inter-individual control of ongoing behaviour by abstracting from particular aspects of behaviour. The results support the conclusion that this is possible and meaningful, but we must, nevertheless, be prepared to face difficulties and sources of error. In order to apply informational statistics, for example, a discrete time scale is required; classification of behavioural transitions rests heavily on the adequacy of the segmentation of ongoing behaviour, while the identification of the moments in time defining this segmentation is itself subject to error. Another difficulty is associated with the use of serial numbers as a time scale: the number and type of intra-individual transitions will be affected by the behavioural rates in other individuals, which can vary independently. However,

for small groups such as triads, it is unlikely that measures of covariability will represent artificial effects in a significant degree. Equally important is the fact that the relationship between two behavioural states separated by a time-mark may be spurious: reactions in a reference monkey with respect to a partner may be anticipatory in some cases and be subject to a certain delay or latency in other cases. Merely relying on the physical borderline between adjacent behaviours in such cases may lead to incorrect associations. To illustrate another difficulty, consider the following combination of preceding and following events. Monkey A sits down grooming itself, and monkey B grunts at A. A then stands up and goes to C (or just goes away to sit elsewhere). A's following behaviour is clearly a reaction to B. But the observable orientation of A's behaviour is towards C (or towards no-one at all). According to our criteria for observable orientation we would classify this event as an instance of the combination "partner directed towards reference subject + reference subject not directed towards partner".

The problems illustrated by the foregoing examples are mainly a result of the combination of the following aspects. Firstly, most techniques for data analysis in ethology, and also much of the mathematics for model building, require a relatively simple dependent variable, preferably unidimensional, since the number of the behaviours to be processed is already rather high. Secondly, the ordinary ethogram is normally a rather heterogeneous collection of items, not composed in accordance with sufficiently formal principles to warrant being treated as a consistent set. Consequently, elements in an ethogram differ in many formal dimensions (such as the possibility of an arbitrary duration; the way they imply or exclude preceding and following behaviour; or the way they imply or exclude concurrent behaviours in others). Thirdly, a description of ongoing behaviour by means of an unidimensional ethogram does not do justice to the actual complexity of behaviour. Most ongoing behaviour in a social situation is of a rather complex nature, at least in primates. Monkeys are able to do several things simultaneously, i.e. to perform several independent acts distributed over one or more objects or partners at the same time. In spite of these difficulties, our approach

seems capable of sufficiently encompassing certain relevant aspects of social behaviour: the highest residual variability we observed was 39% (subject Ne in Table 7.2), so that more than 60% of ongoing behaviour can always be related to the factors incorporated in a model of first-order inter- and intra-individual behaviour transitions.

CHAPTER 8

A GENERAL PROCEDURE FOR MULTIVARIATE ANALYSIS OF NOMINAL DATA BY MEANS OF INFORMATIONAL STATISTICS

Any system of p interacting variables or state sets (not necessarily different) can be analysed by means of information-theoretical statistics. An informational analysis consists principally in relating distributions of (nominal) variables to each other. In general two approaches are possible, analogous to the basic types of multivariate analysis of metric data: 1) factor analysis and multiple correlation analysis, and 2) regression analysis and analysis-of-variance. In the first approach the system of p variables is not partitioned in independent and dependent variables. The overall constraint existing in the total set of variables is expressed by means of transmission measures (Watanabe, 1960; Garner, 1962; Ross, 1962; Fhanér, 1966; Char-Tung Lee, 1971; Broekstra, 1978). Similarly the total constraint present within any subset of the variables or between any two subsets can be expressed. Since no particular linear model is assumed, all kinds of higher-order covariability terms may be present. In the second approach some variables are interpreted as independent or predictor variables and the remaining ones as dependent or criterion variables. An information-statistical analysis-of-variance then can be applied to identify sources of variance, contributing to the variability of the dependent variables (McGill, 1954, 1955; Garner and McGill, 1956; Krippendorff, 1971). In an informational analysis-of-variance both the dependent and the independent variables are nominal, whereas in the usual analysis-of-variance only the independent variables are nominal.

COMPUTATIONAL PROCEDURES

The maximum number of terms in a model with a system of p variables (comprising both the independent and the dependent variables) is 2^p-1; this number is equal to the number of all possible subsets that can be composed from a set of p elements, minus one, for the empty subset. The number 2^p-1 contains p residual variabilites, $\frac{1}{2}p(p-1)$ first-order covariabilities, and a number of higher-order covariabilities and interaction terms. The number of partial covariability terms of a particular size, representing the constraints within a particular number of variables, say m, while the remaining variables are kept constant, is equal to $\binom{p}{m}$ for m = 2 ... p.

The 2^p-1 model parameters must be estimated from combinations of 2^p-1 data parameters, i.e. from the single variabilities of the p variables individually and from the joint variabilities of all possible combinations of variables. The full set of single and joint variabilities can once again be specified by enumerating all the possible subsets of a collection of p elements.

The computational procedures involved in estimating the parameters of the model of interaction sequences developed in chapter 4 will be presented in some detail, together with a few practical suggestions, in the remainder of this chapter. Measures of variability are usually estimated from relative frequencies; joint variabilities or variabilities for a combination of events are estimated from joint frequencies. The required partial covariability measures are derived by adding or subtracting the appropriate single and joint variabilities. Our model focuses on the interaction between a reference subject i and a partner j, as manifested in first-order behaviour transitions. The first step is to define the variables and combinations of variables involved in these transitions and then to compute the variability of their frequency distributions. The resulting data parameters are the quantities a-f shown in Table 8.1. From these data parameters the required model parameters (the quantities j-m in Table 8.1) are easily obtained. The algorithm we used for adding and subtracting the data parameters is presented in Table 8.2.

TABLE 8.1

Informational quantities describing dyadic interaction based on first-order behaviour transitions. a-f: data paramters; j-m: model parameters; g-i: intermediate terms

quantity		formula in text	
a	individual variability of i	$H(I_t)$, $H(I_{t-1})$	(1)
b	individual variability of j	$H(J_t)$, $H(J_{t-1})$	
c	contingent joint variability	$H(I_tJ_t)$, $H(I_{t-1}J_{t-1})$	(4)
d	sequential joint variability (intra-individual)	$H(I_tI_{t-1})$	(2)
e	sequential joint variability (inter-individual)	$H(I_tJ_{t-1})$	(3)
f	total joint variability	$H(I_tI_{t-1}J_{t-1})$	(4)
g	autocovariability	$T(I_t:I_{t-1})$	(2)
h	cross-covariability	$T(I_t:J_{t-1})$	(3)
i	total sequential covariability	$T(I_t:I_{t-1}J_{t-1})$	(4)
j	partial autocovariability	$P(I_t:I_{t-1})$	(6)
k	partial cross-covariability	$P(I_t:J_{t-1})$	(7)
l	interaction covariability	$P(I_t:I_{t-1}J_{t-1})$	(5)
m	residual variability	$U(I_t)$	(8)

The numbers in the last column correspond with those of the formulae in chapter 4

TABLE 8.2

Algorithm for computing the model parameters from the data parameters for the quantities defined in Table 8.1. The first step consists of adding the individual variability (a) and the contingent joint variability (c) and subtracting the total joint variability (f), which results in the total sequential covariability (i); etc.

step	data parameters										model parameters				
	a	b	c	d	e	f	g	h	i		j	k	l		m
1	a		+c			-f	=		i						
2	2a			-d			=	g							
3	a	+b			-e		=		h						
4							-g		+i	=		k			
5								-h	+i	=	j				
6							g	+h	-i	=			l		
7	a										-j	-k	-l	=	m
check	a								-i					=	m

There are other ways to derive the model parameters, in particular by the use of conditional probabilities and, correspondingly, conditional variabilities (Altmann, 1965; Chatfield, 1970). This approach might be preferable for behavioural sequences, which have an inherent notion of time ranking. The autocovariability, $T(I_t:I_{t-1})$ for instance, can be defined in several ways:

$$T(I_t:I_{t-1}) = H(I_t) + H(I_{t-1}) - H(I_tI_{t-1}) \quad (2)$$

$$T(I_t:I_{t-1}) = H(I_t) - H(I_t\ I_{t-1}) \quad (2')$$

$$T(I_t:I_{t-1}) = H(I_t) - H(I_{t-1}\ I_t) \quad (2")$$

The relation between the physical referents of I_t and I_{t-1} is not symmetrical, the direction of causation being from I_{t-1} to I_t. Only definition 2' preserves the intuitive meaning of the situation. The right hand side of 2" denotes exactly the same autocovariability but is physically nonsense. Equation 2 is neutral: the natural order of the variables I_t and I_{t-1} does not matter, although the subscripts of time naturally admit only one physically meaningful interpretation. The reason for using formulae such as equation 2 is that they present the actual computational formula: it is much simpler to write a program for information measures using single and joint probabilities than conditional probabilities.

For small state sets or repertoire sizes ($m \leqslant 10$), it is possible to assemble the data (frequencies) in a three-way contingency table, whose dimensions are defined by the single variables I_{t-1}, J_{t-1} and I_t. The cells of this matrix contain the frequencies of the highest order event, in our case the combination $I_{t-1}J_{t-1}I_t$. The frequencies of paired and single events are generated as the marginal distributions which result from summing the cells over the appropriate dimensions.

For larger repertoire sizes the construction of a multidimensional contingency table is quite laborious, even for a computer. Since our own work on the social behaviour of monkeys involves a repertoire of 95 behaviour patterns we used another strategy. A general program for computing a variety of informational quantities, "INFAN", was developed, written in Fortran IV. The basic principle is simply to sort, combine and count lists of the relevant events, defined by format-specifications for the input protocol, without using the numerical content of the behaviour codes. Details on this program are given in the last section of this chapter.

A practical problem concerns the relationship between the number of elements in the state set (repertoire size) and the size of sample needed for reliable estimates. It is possible to compute in advance, for a given repertoire size, the sample size necessary for stating with reasonable certainty that observed variability measures are equal to the true or population value

within given confidence levels (Nemetz, 1972). For instance, with a state set of 50 elements and a sample size of more than 2,500,000, we may state of the 95% confidence level that our observed H-value has an error of less than 0.28 bits (= less than 5% of the maximum H-value). Much larger samples are required for transmission measures where combinations of events are to be observed. The above only applies to independent sampling, a condition not normally fulfilled in the case of behaviour sequences. As it is clear that the price for such a guarantee often far outweighs the need for the information supported by it, the following suggestions can be useful. As the number of observations in a sample depends on the actual size of the repertoire, it is convenient to set an upper limit to the repertoire size. Quantitative methods for estimating a suitable repertoire size are discussed by Fagen and Goldman (1977). Sample size is also dependent on the number of combined events that can occur: a given sample is more powerful when it has fewer degrees of freedom for combinations of behaviour. A quantitative method for establishing the actual number of degrees of freedom for a given repertoire and sample size is presented in the next section. Finally, it is also useful to evaluate the effect of a given sample size on the accuracy of the statistics based on it. A method for this purpose is also presented in the next section.

STATISTICAL PROCEDURES

As far as statistical theory is concerned there are several problems associated with information measures. Particular examples are, a) correction for bias, confidence limits and sample size; b) tests of the significance of variability measures (H) against zero or against other null hypotheses; and c) tests of transmission measures against zero or other hypothesized values. These problems have not as yet been solved in a sufficient degree to allow a matter-of-fact application of information-statistics in ethology. After a brief mention of some relevant references we outline a relatively simple procedure for testing information-statistics, especially covariability measures.

The question of bias correction was reviewed by Macrae (1971). Nemetz (1972) provided a formula for establishing the sample size required to ensure that, the probability of the difference between the true and estimated (co)-variability remains below a given level. A procedure for testing information measures by means of exact sampling probabilities was presented by Cronholm (1963), but his method is only suitable for small samples. For testing transmission measures against zero, a chi-square approximation has been described (McGill, 1954; Chatfield, 1970). This method is, however, rather demanding: apart from the requirement of independent sampling which is not usually met in transition tables for behaviour sequences, the sample size is often too small and the number of degrees of freedom difficult to establish. Recently Fagen (1978) developed a method for bias correction, confidence limits and hypothesis testing which does not suffer from these shortcomings.

Our procedure was likewise motivated by the need to overcome the difficulties associated with the application of information theoretical statistics. We used a Monte Carlo procedure which consists essentially in computing the value of the transmission to be tested along with the value of the null hypothesis from the same set of data. As a by-product information on the number of degrees of freedom associated with the transition tables is generated. The procedure is based on the following considerations.

The estimate of any covariability term will be affected by error due to insufficiency of the sample. Testing an observed covariability, $\hat{T}_{obs}$, against a transmission expected under the null hypothesis, T_{null}, is equivalent to assessing the probability that $\hat{T}_{obs}$ lies at a certain distance from T_{null} well beyond sampling error. In our case, we want to compare observed covariabilities with zero covariabilities, i.e. with values that would prevail under conditions of random (= no) transmission. Or rather, to make a less rigorous null hypothesis, with covariabilities reflecting any (unknown) condition apart from the one that supposedly produces $\hat{T}_{obs}$. For instance, we want to test $\hat{T}_{obs}$, which reflects causal conditions c_1 and c_2 against T_{null}, which reflects condition c_1 only, where c_2 is assumed to represent

social interaction or communication and c_1 assumed to reflect random or unknown conditions (c_1 is defined simply as not c_2). We can in fact turn the argument around: if it is possible to obtain a suitable T_{null} and its variance from the same sample that produces $\hat{T}_{obs}$, the difference between $\hat{T}_{obs}$ and T_{null} may easily be evaluated. It is indeed possible to sample a number of estimates of T_{null} from the data and compute the corresponding sampling variance. We must still make an assumption, however, on the nature of this sampling procedure. In the case of zero transmission, i.e. for transmission under purely chance conditions, we may assume that the estimates of T_{null} are exponentially distributed. In the case of transmission under unknown conditions we may assume a normal distribution around a positive mean expected value of T_{null}. In our procedure the actual mean ($= \hat{\bar{T}}_{null}$) and the standard deviation of this distribution (= sampling error, $\hat{S}_{Tnull}$) were determined by computing several estimates of T_{null} from the same sample. The data consisted of a sample of N combinations of events, and as we were dealing with transmission measures the marginal distributions provided by this sample were kept fixed. We computed from the data a certain number, say r, of transmission values, which were assumed to be valid under the conditions of the null hypothesis. The following procedure was adopted. For the first run an inter-behaviour lag, l = 10, was chosen, on the assumption that the dependencies between the behavioural states at time t and t-10 were not the same as the ones between immediately adjacent behaviours. For the next run, l was set at 11, and so on until l reached 20. We therefore obtained ten values for estimating T_{null} and its sampling error. By referring to the normal distribution table we could see whether the observed transmission $\hat{T}_{obs}$ was within the interval between $\hat{\bar{T}}_{null}$ and $\hat{\bar{T}}_{null} + 3\ \hat{S}_{Tnull}$. (It should be noted that if the successive lagged covariabilities vary systematically due to a certain periodicity, the variance of T_{null} will be overestimated and the resulting test will tend to be conservative.) Several alternatives to this technique are possible, based on the same rationale. Theoretically, the best procedure is to select r sets of N random combinations of first and second behaviours, by vary-

ing the lags between the behaviours at random; i.e. in every run each consecutive event in the sample is taken once as first event and the second event of the combination found by a random selection of the lag between the events. Another procedure is to keep the lags fixed during each of the r runs but to vary them at random between runs (r should be large enough to neutralize the effect of small lags). The method of lagged covariabilities was chosen because of its computational simplicity.

The procedure offers the opportunity (by making r sufficiently large) to estimate the sampling error of the statistics associated with samples of given size N. Moreover, the computation of lagged covariabilities also provides information necessary for estimating the actual number of degrees of freedom for first-order transitions associated with the given ethogram. The reasoning for this is as follows. Positive frequencies of first-order intra-individual transitions are assumed to reflect only a fraction of the physically and psychologically possible behavioural combinations; this fraction is called p. The zero frequencies will be made up from possible but as yet unobserved combinations (a fraction q) and from impossible and therefore unobserved combinations. We have therefore p+q behaviour combinations providing the actual number of df. How can we estimate q, the number of possible transitions we missed through imperfect sampling? When we take transition frequences for behaviours with a large lag, e.g. ten or twenty intervening behaviours, we may assume that the intrinsic constraints no longer apply. Therefore, the number of positive frequencies should be larger than p, as it contains nonsense transitions as well, due to the removal of intrinsic constraints. The zero transitions, however, will only reflect sampling insufficiency and hence may be used to estimate q. It should be stressed that this estimate of (p+q) is not independent of the sample size N: it will be the more accurate, as N increases up to a certain limit, where q=0. However, we are not dealing with the accuracy of an estimate as a function of sample size, but with separating the effects of sampling insufficiency and intrinsic constraints for a given sample size.

To compare two transmission values, $\hat{T}_{obs1}$ and $\hat{T}_{obs2}$, from

different samples (e.g. obtained under different experimental conditions) we have to deal with two problems: a) scale: the samples may have different actual maxima for the transmission, and b) unequal sampling insufficiency: the estimates in the one sample may be better than the corresponding estimates in the other. The first problem requires standardization of the observed transmission with respect to the range of the possible values. The actual maximum transmission between two variables, X and Y, is a function of the individual variabilities; it is equal to the smaller of H(X) and H(Y). In general, this maximum will differ for each sample; moreover, it is likely to vary according to differences in experimental conditions. As a consequence, it is difficult to determine a maximum for the transmission between X and Y based on observed values of H(X) and H(Y). To circumvent this problem we decided to assign for each sample the absolute maximum transmission, equal to the smaller of the maximum single variabilities. The latter are in turn a function of the number of elements in the state set. Because we assumed the same repertoire, containing m elements, for all individuals the maximum individual variabilities are equal and, consequently, the maximum possible transmission for a given m is equal to $H_{max} = \log_2 m$. It should be recognized that although this treatment of the problem of scale is both rational and pragmatic, it is not entirely realistic: the upper limit for transmission established in this way is based on a maximum variability of behaviour that seldom, if ever, will be observed.

The problem of unequal sampling insufficiency was handled by assigning to each of the observed transmissions a sampling error equal to that of the transmission under the null hypothesis, computed for each sample according to the procedure outlined in the paragraph on testing single transmission values above. We have thus two observed transmission values, $\hat{T}_{obs1}$ and $\hat{T}_{obs2}$, each having its own sampling error, $\hat{S}_{Tnull1}$ and $\hat{S}_{Tnull2}$.

It seems reasonable to assume that estimates of the true transmission, based on a number of samples of the same (given) size, are normally distributed, with a standard deviation equal to the sampling error associated with samples of the given size. (This

is equivalent to assuming stationarity.) We can therefore compare the transmission values by means of the usual t-test for two means.

To summarize, we devised a Monte Carlo procedure for testing informational measures, particularly transmission measures, because at present statistical theory is not sufficiently developed to cover all cases for which specific tests are necessary. At the cost of a number of assumptions, which do not however deviate from established statistical practice, it permits conclusions to be drawn regarding the significance of informational quantities for a given sample.

DESCRIPTION OF PROGRAM "INFAN"

Function of INFAN

"INFAN" computes the variability, H, for any combination X of variables, according to the formula:

$$H(X) = \sum p(x_1) * {}^2\log p(x_1)$$

where x_1 is a particular combination of the values of the variables constituting the set X, and $p(x_1)$ is a probability distribution for the events x_1, estimated from the relative frequencies of the events in the input protocol.

Input (FTN2.DAT). The input file is a data matrix with the rows consisting of observational or data-units and the columns elements of a vector of nominal variables, which define properties or particular states of the observational unit. The general format of the data matrix is an array of "NDAT" rows of, at most, 80 digits. The actual identification and labelling of the data-units and the elements of the vector variable are to be provided by the user. For instance, rows may be subjects and columns may be measurements; or, in the case of interaction sequences such as described in chapters 4 and 5, rows may be successive points of time and columns may be the behavioural states of one or more subjects. The data matrix is preceded by two records containing identification of the dataset (format: 80A1)

and a record containing the number of data-units (= records) in the input file (format: I5). The codes for the elements of the vector variable must be numerical. The code for the relevant event X consists of a number of digits to be taken from the state descriptions in one or more rows (= records) of the data matrix, according to a variable format.

Operation. The following input-parameters have to be specified by the user at the terminal.
- format-parameter: 0 or 1; when this parameter is entered as 0, the format for the requested combination of variables has to be provided by the user; when it entered as 1, a predefined set of one or more formats is read by "INFAN" from a format-file and all the variabilities defined by the format-list are computed.
- number of digits per event: the total number of digits in the desired combination of variables (I5).
- number of records per event: the number of data-units over which the separate variables constituting the event are distributed.
- list of event types: 0 or 1; a list of different combinations of the values of the variables in the event may be obtained by entering this parameter as 1.
- frequency and variability per event type: 0 or 1; for each different combination of variables, the frequency, relative frequency (p) and the quantity $p.^{2}\log p$ are provided on the output file when this parameter is entered as 1.
When the format-parameter is equal to 1, indicating that the event-formats are to be taken from a special format file, the remaining input-parameters must also be present in that file (see below); they do not then need to be specified on the terminal.

Output (FTN4.DAT). Standard: total number of different events (= event types), variability H of the frequency distribution of the event types, and the maximum variability for the specific number of event types present in the input-protocol.
Optional: list of event types; frequency, relative frequency and variability of every event type.

Predefined formats. "INFAN" can be used for computing the variability of an event that is defined at the terminal, or for computing a number of variabilities listed on a separate format file (FTN95.DAT). The format-file has to be composed as follows. First three records: vacant (80A1). Remaining records: for each variability the following three successive records; 1) description and formula of the variability; 2) input-parameters (otherwise entered via the terminal); and 3) format of the required event.

Example. Table 8.3 shows a part of the kind of data matrix obtained in our experiments. Rows are successive points in time and columns contain the state descriptions of one or more subjects. Let us suppose that we want to compute the variability H(X) for the following events:

a) the current behaviour of subject 1 (15, 45 etc.)
b) the current and preceding behaviour of subject 1 (4515, 6945);
c) the current behaviour of subject 1 and the preceding behaviour of subject 2 (4502, 6902 etc.).

At the terminal we would specify the parameters for these events as follows:

a) ....0....2....1
   (10X, 2I1)
b) ....0....4....2
   (10X, 2I1, /, 10X, 2I1)
c) ....0....4....2
   (19X, 2I1, /, 10X, 2I1)

The specifications for a) have the following interpretation. The zero indicates that the event is defined by the format of the following line; the 2 indicates that its code consists of two digits, and the 1 indicates that the digits are all in one record (dots are used to indicate blanks; the format specification is in Fortran; for instance, the format for a) means: skip the first 10 characters of each record and then take two integers of one digit). Instead of specifying the parameters for the events a, b, and c individually, for each run of the program, it would have been possible to list them in a separate format-file.

TABLE 8.3

Example of a data matrix containing interaction sequences

record	time			subj 1			subj 2			subj 3		
	h	m	s	b	l	o	b	l	o	b	l	o
1	09	48	47	15	1	14	02	1	20	14	2	14
2	09	48	53	45	1	3	02	1	20	14	2	14
3	09	48	54	69	8	3	02	1	20	68	2	1
4	09	48	56	80	9	3	02	1	20	55	10	1
5	09	48	59	69	7	3	02	1	20	68	7	1

h = hour *b = behaviour* *subj = subject*
m = minute *l = location*
s = second *o = orientation*

Technical details

Procedure. The program selects "ND" digits from the state description on one or more input records (according to a variable format specified by the user); a string of "ND" digits will be called an eventstring or an event. When the total number of events in the input file (= "NEVT") is too large to be accommodated by the fixed size internal buffer, the input is segmented into "NIS" input segments, each containing "NEVIS" events. The events in each input segment are read and recoded (2 digits = 1 numerical code, to be stored in 1 byte) and stored in a one-dimensional buffer-array. In the next step the events are sorted (actually only the addresses of the events are sorted) by an algorithm based on radix sorting. On request (by the appropriate input-parameter) the sorted events of the input segment may be counted and listed on file FTN80.DAT. The sorted events are put on a direct-access bufferfile on Disk (FTN90.DAT). When all input segments are processed, the resulting event lists are simultaneously read back into the internal buffer in separate parts, combined and counted. The variability of the events is subsequently computed.

Memory constraints. The internal buffer-array is assumed to consist of 16,000 1-byte locations (= 8,000 words in a PDP 11 computer). Several subroutines of "INFAN" require up to 256 bytes additional working space. The following maxima are set:
- number of digits per event ("ND"): 60
- number of input segments ("NIS"): 6

The maximum for the total number of events in the input file ("NEVT") is accordingly given by the formula:

NEVT.LE.6*(16000/((ND+MOD(ND,2))/2 + 4))

Therefore, when "ND" = 60, "NEVT" may not exceed 2,820; and when "ND" = 4, "NEVT" should not exceed 16,000. (It should be noted in passing that for eventstrings of 3 digits and less "INFAN" is a rather inelegant program: these can be sorted and counted directly by using the numerical equivalent of the 3-digit code!)
Data records may not exceed 80 positions (characters); a maximum of 60 positions of each data-unit is to be used for coding the vector variable, nor should the format-specification exceed 80 characters.

GENERAL COMMENT

The program "INFAN" was written in Fortran IV, for use on a PDP 11-series computer, under the operating system RT-11. It requires about 20 Kbytes core memory for internal data manipulation. The program is run via a terminal; the I/O-files are on Disk. From the description of "INFAN" it will be evident that interaction sequences represent only one specific kind of input for the program; a transition matrix is just one of the many combinations of variables that are possible. When the input for "INFAN" consists of consecutive behavioural state descriptions for a number of interacting subjects, the program can be used to compute measures of variability for virtually any combination of events (inter- and intra-individual), up to any reasonable order or complexity; "INFAN" can therefore be applied to a broad class of information-statistical models. Moreover, lagged correlations, for events separated by any reasonable lag, are also possible,

which proved particularly convenient for purposes of hypothesis testing (see preceding section). For the sake of completeness it may be added that "INFAN" is less complex, requires less storage and is more general and versatile than any other program currently available for information-statistical analysis (Dale et al., 1970; Hayes-Roth and Longabaugh, 1972; Aspey, 1977).

CHAPTER 9

SOME DATA ON THE NEUROBIOLOGY OF THE CAUDATE NUCLEUS

The caudate nucleus or the striatum (caudate nucleus + putamen) is the most extensive part of the basal ganglia complex; it is, in fact, the largest subcortical cell mass in the mammalian brain (Nieuwenhuys, 1977). The nucleus has been the object of investigation ever since the development of experimental neurophysiology (see references in Ward, 1968) and continues to be so. In recent years interest in this nucleus continues to grow, as is evidenced by the number of symposia devoted to its structure and function (Yahr, 1976; Cools et al., 1977; Hassler and Christ, 1979*; Divac, in press).

In this chapter some neurobiological data will be reviewed as an introduction to chapters 10 and 11.

ANATOMY AND CHEMISTRY

Since several excellent reviews on the anatomy and physiology of the caudate nucleus are available (Mettler, 1968; Kemp and Powell, 1971; Mehler and Nauta, 1974; Carpenter, 1976; Nieuwenhuys, 1977; Grofová, in press), I will merely summarize the anatomical findings illustrated in Fig. 9.1 and add some comments on the most recent anatomical and neurochemical data.

---

*R. Hassler and J.F. Christ (eds.): Basal Ganglia - Cellular and Functional Aspects. Abstracts of the International Symposium on Basal Ganglia, Frankfurt a.M., July 10-13, 1977. Basel, S. Karger (= Appl. Neurophysiology, vol. 42, no. 1-2, 1979).

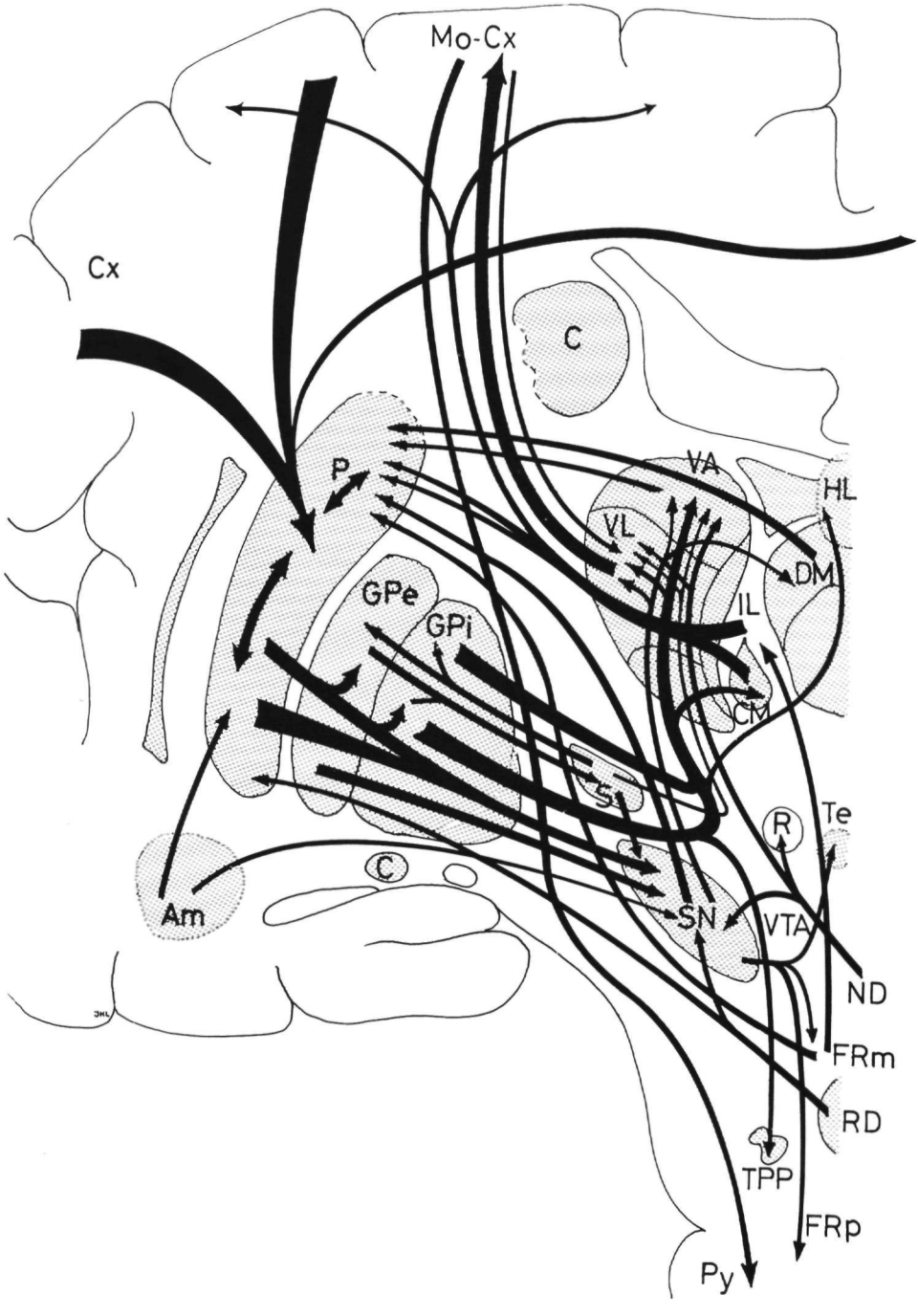

Mo-Cx
Cx
C
P
VA
HL
VL
DM
IL
GPe
GPi
CM
SI
R
Te
C
Am
SN
VTA
ND
FRm
RD
TPP
FRp
Py

Fig. 9.1

Schematic representation of the anatomical input-output relations of the striatum (caudate nucleus + putamen)

Abbreviations

Am : *amygdala*
C : *caudate nucleus*
CM : *centrum medianum thalami*
Cx : *cortex*
DM : *dorsomedial nucleus of the thalamus*
FRm : *formatio reticularis of the mesencephalon*
FRp : *formatio reticularis pontis*
GPe : *globus pallidus externus*
GPi : *globus pallidus internus*
HL : *habenular nucleus*
IL : *intralaminar nuclei of the thalamus*
Mo-Cx : *motor cortex (areas 4 and 6)*
ND : *nucleus dentatus of the cerebellum*
P : *putamen*
Py : *pyramidal tract*
R : *nucleus ruber*
RD : *nucleus raphes dorsalis*
S : *nucleus subthalamicus*
SN : *substantia nigra*
Te : *tectum mesencephali*
TPP : *nucleus tegmenti pedunculopontinus*
VA : *nucleus ventralis anterior of the thalamus*
VL : *nucleus ventralis lateralis thalami*
VTA : *ventral tegmental area*

Note
Although the diagram shows only the extrinsic connections of the putamen, the same relations apply to the caudate nucleus

Afferent and efferent connections

The caudate nucleus receives afferent fibres from the cortex, the thalamus (nucleus dorsomedialis, nucleus ventralis anterior, nuclei intralaminares and centrum medianum), the substantia nigra, the reticular formation of the mesencephalon, the nucleus raphe dorsalis, and the amygdala. Its main output fibres terminate in the globus pallidus and in the substantia nigra. These input-output connections form part of a complex pattern of further connections and feedback loops (Nieuwenhuys, 1977).

By means of recently developed neuroanatomical techniques such as horseradish peroxidase tracing and autoradiography, it has been shown that the extrinsic connections of the caudate-putamen are very elaborate and intricately organized. Some ten years ago it was established that all cortical areas project to the caudate-putamen in a topographical manner and that the projections from the frontal and parietal cortex are more extensive than those from other cortical areas (Kemp and Powell, 1971). It now appears that the prefrontal cortex projects predominantly to the caudate nucleus (Goldman and Nauta, 1977), while the outflow of the motor and sensorimotor cortex is primarily directed at the putamen (in monkeys; Künzle, 1975; Jones et al., 1977). Moreover, projections from the prefrontal cortex are distributed over the whole caudate nucleus (Goldman and Nauta, 1977) and afferents from the sensorimotor cortex terminate all over the putamen (Jones et al., 1977). The topographical relations between the cortex and the striatum have been further complicated by the finding that reciprocally connected cortical areas have a common projection in the striatum and that a single cortical area terminates in different striatal areas (Yeterian and Van Hoesen, 1978). The subcortical afferents to the striatum are also more extensive than previously thought, especially the afferents from the thalamus, which include afferents from the nucleus ventralis anterior and the dorsomedial nucleus; striatal afferents also originate in the amygdala (nucleus basolateralis), the ventral tegmental area (which is continuous with the substantia nigra), and the retrorubral area (in cats; Royce, 1978b). Moreover, autoradiography has revealed that cortical and subcortical afferents

(especially from the centrum medianum of the thalamus) may terminate in the striatum in similar patterns and interlock with one another in a complex anatomical mosaic (in the cat; Royce, 1978a; in monkeys; Kalil, 1978).

From anatomical and electrophysiological data it is also clear that the striatum is a component of a system that is involved with several other anatomically or functionally defined systems. In the intralaminar nuclei of the thalamus the output of the basal ganglia merges with the ascending reticular formation. The nucleus ventralis anterior and the nucleus ventralis lateralis of the thalamus receive output from both the basal ganglia and the cerebellum (Frigyesi, 1975a, b; Purpura, 1976; Batton III et al., 1977). Finally, the nucleus habenularis lateralis may be a meeting point for extrapyramidal and limbic system output (Kim et al., 1976; Herkenham and Nauta, 1977).

Intrinsic structure

The intrinsic organization of the caudate nucleus has been investigated by two research groups: Pasik and DiFiglia (Pasik et al., 1976, 1979; DiFiglia et al., 1978), using both light microscopy and electron microscopy, and Rafols and Fox (Rafols and Fox, 1979*) using Golgi preparations.

DiFiglia and Pasik distinguish at least six types of neurons in the neostriatum of monkeys. 1. Spiny I cells, of medium size; their dendrites are about 200 μm long with many spines and no varicosities; their axon is long and has many collaterals. 2. Spiny II neurons, large or medium sized, with rather long dendrites (600 μm) having a few spines and no varicosities; the axons also are long and have some collaterals. 3. Aspiny I cells, of medium size, that have shorter dendrites (150 μm) with many varicosities; the axon is short and arborized. 4. Aspiny II neurons, larger than aspiny I neurons, with dendrites of about 250 μm. 5. Aspiny III neurons, of medium size, with short den-

*Rafols, J.A. and Fox, C.A. (1979) Fine structure of the primate striatum. Appl. Neurophysiol. 42, 13-16.

drites (150 μm), that rarely have spines or varicosities; the axons are short and arborized. 6. Neurogliform, small cells, with rather short dendrites (70 μm) having some varicosities.

Rafols and Fox (1979) distinguish the following types of neurons (in the neostriatum of rhesus monkeys). 1. Medium neurons with many dendritic spines (= spiny I neurons of DiFiglia and his coworkers). 2. Medium neurons with fewer dendritic spines (= spiny II neurons of medium size). 3. Large neurons with many dendrites (= aspiny II cells). 4. Large neurons with fewer dendrites (= spiny II, large form). 5. Small aspiny neurons (= aspiny I and III, probably). 6. Medium neurons with radiating beaded dendrites (not described before).

The afferent fibres of the neostriatum have been described as being of four types (DiFiglia et al., 1978). Each type of extrinsic fibres appears to be associated with a particular area of origin. Type 1 fibres have thick axons with varicose branches and probably originate in the diencephalon or in the brain stem. Type 2 afferents are thick, with large, grape-like appendages and may be of thalamic origin. Type 3 axons are thin and have beaded branches; they may arise from the substantia nigra and perhaps also from the dorsal raphe nuclei and the locus coeruleus. Type 4 fibres are thin and have side twigs; they are most probably of cortical origin. These data have been incorporated by the authors in a tentative scheme for the local circuitry of the neostriatum (Pasik et al., 1979), in which the spiny neurons (I and II) are thought to be efferent fibres and the aspiny neurons interneurons.

Chemical composition and transmitters

The neuroanatomical picture is complemented by recent neurochemical investigations, most of which were done in rats. The striatum is known to be rich in several (putative) neurotransmitter substances, or neuroregulators, notably dopamine (DA), serotonine (5HT), acetylcholine (ACh), gamma-aminobutyric acid (GABA) and substance P (Lloyd, 1975; Vogt, 1975). Several of these substances are associated with identified striatal afferents and efferents. The localization of DA in nigrostriatal neurons is already widely documented (reviewed in

Cools, 1977). It appears that glutamate is the transmitter of the cortical afferents to the striatum (Divac et al., 1975; McGeer et al., 1977, 1978). There is also growing evidence for a substance P containing pathway from the striatum and the pallidum to the substantia nigra (Brownstein et al., 1977; Hong et al., 1977; Kanazawa et al., 1977; Fonnum et al., 1978; Jessel et al., 1978; Scally et al., 1978). Serotonin may well be the transmitter in the pathway from the raphe dorsalis to the striatum (Miller et al., 1975; Samanin et al., 1978).

There exist significant regional differences in the occurrence of these neuroregulators and their enzymes in the striatum, both in the rat and in the cat. Serotonin terminals are mainly located in the ventrocaudal area, and their density decreases progressively in the caudo-rostral direction (Guyenet et al., 1977; Ternaux et al., 1977). Dopamine is mainly found in the rostral part of the striatum, and to a lesser extent in the caudal part (Guyenet et al., 1977; Scally et al., 1978). There is evidence of two types of dopamine receptors in the striatum, possibly differentially distributed as well (Cools and Van Rossum, 1976; Norcross and Spehlmann, 1978). Neurons containing GABA and substance P are mainly concentrated in the caudal part of the striatum (Scally et al., 1978). The level of acetylcholine (ACh) in the neostriatum is higher than elsewhere in the brain (Hoover et al., 1978). ACh and choline acetyltransferase (ChAT) occur predominantly in the rostral and centro-lateral area of the neostriatum (Guyenet et al., 1977; Scally et al., 1978). The cholinergic receptors in the neostriatum are mainly of the muscarinic type (Yamamura et al., 1974; Kuhar and Yamamura, 1976; Morley et al., 1977). There is some controversy concerning the origin of the cholinergic neurons in the neostriatum (Olivier et al., 1970; Poirier et al., 1974). However, ACh is quite probably located in interneurons, as the content of ACh, ChAT and acetylcholinesterase in the neostriatum is not significantly altered by discrete lesions of projections to the neostriatum (ventral thalamus, substantia nigra, brain stem, cortex) (McGeer et al., 1973; Butcher and Butcher, 1974; Butcher, 1977). Somewhat contradictory to this result is the observation that when electrolytic

lesions are made in the nucleus parafascicularis of a rat's thalamus, a marked reduction in ChAT activity in the head of the neostriatum occurs (Simke and Saelen, 1978). However, in this study the possibility of retrograde or transneuronal degeneration was not excluded. Moreover, it was shown by immunohistochemistry that ChAT containing neurons in the striatum are Golgi type II neurons (McGeer et al., 1974; cf. also Cheyney et al., 1975). We may therefore assume that cholinergic neurons in the striatum are indeed interneurons. (The converse is not true: some interneurons may be GABA-ergic (Racagni et al., 1977).)

FUNCTION IN BEHAVIOUR

The function of the caudate nucleus in behaviour has been the subject of much research and speculation. It was early on conjectured that this nucleus is involved in motor functions (for reviews see: Jung and Hassler, 1960; Ward, 1968), based particularly on clinical symptoms of motor disturbances. As the techniques of neurobehavioural research became more sophisticated the list of behavioural or psychological processes in which the caudate nucleus was thought to be involved, grew longer and more diverse. Concurrently, the theoretical accounts of the organization of behaviour and of psychological phenomena became more sophisticated; this too has been reflected in the kind of functions ascribed to the caudate nucleus. During the last ten years it has been suggested that the caudate nucleus is involved in all the following functions or processes: the identification of "non-signals" or irrelevant stimuli (Ursin et al., 1969), generalized behavioural inhibition (Klemm and Dreyfus, 1975; Neill, 1976), arousal (Kirkby, 1973), the flexibility of response under stress (Kirkby, 1969), the organization of conditioned motor reflexes (Adrianov and Shungalev, 1978), the temporal programming of response components (Wilburn and Kesner, 1974), response-chaining (Cools, 1973), the organized expression of species-typical behaviour (MacLean, 1978), spatial orientation (Winocur and Mills, 1969), egocentric or absolute localization (Potegal, 1972), avoidance learning (Thomas and Hill, 1973; Kirkby and Polgar, 1976), (maze) learning and memory (Kirkby, 1978), short

term memory, retention and (retrograde) amnesia (Herz et al., 1975), "complex" or "cognitive" functions (Divac et al., 1978), reinforcement and reward (Broekkamp et al., 1977; Neill et al., 1978), intracranial self-stimulation (Redgrave, 1978), paradoxical sleep (Corsi-Cabrera, 1975), and the regulation and control of growth (Schiff and Carter, 1977). This list of references represents a sample of reports on experimental results mostly obtained by a single experimental technique (lesion, electrical or chemical stimulation) in one or a limited number of test situations (delayed alternation, avoidance learning, extinction etc.). Over the same period several reviews have been presented, varying in their coverage of the experimental data: some are principally summaries of an author's own research supplemented with general conclusions (Rosvold, 1968; Divac, 1972, 1977; Potegal, 1972; Frigyesi, 1975a, b; Bowen, 1976; Hassler, 1978). Other articles attempt to provide a truly general survey of the clinical and experimental data (Laursen, 1963; Mettler, 1967; Barbeau, 1972; Villablanca, 1975; Webster, 1975; Teuber, 1976). Some comments on the various approaches to the problem of the function of the caudate nucleus are given in Cools and Van den Bercken (1977).

Two points clearly emerge from recent discussions on the striatum: its function is a broad one, not limited to direct motor control; and its function is quite complex. It may be said that the latter statement is about the only one that will be agreed with by almost everyone in the field! The following anthology of quotations may serve to substantiate this claim. The order of the quotations is chronological, except for the last two, which effectively summarize all the preceding ones.

Mettler (1967): "The presence of the striatum enables the organism to engage in much more complex activities" (than single movements) "largely as a result of freeing it from the domination of the muscle afferent inflow." "The striatum is involved in the organism's effort to relate itself to its environment"..... (It) "appears to act as a mechanism that frees the organism from proprioceptive (and to a lesser extent, visual) dominance and thus puts it in a position to react to alternative stimulus configura-

tions, i.e. to make choices."

Rosvold (1968): "The frontal cortex and the head of the caudate nucleus have similar functions. These functions appear to be involved principally with the modulation of activity in the motor system which is necessary for an animal to accurately direct his behavior. At least two such functions are dissociable, each related to a different cortical-subcortical system. The orbital frontal cortex and ventrolateral sector of the caudate appear to determine whether or not a response will occur, while the lateral frontal cortex and anterodorsal sector of the head of the caudate determine where it will occur."

Potegal (1969, 1972): "..... the caudate nucleus functions as part of an egocentric localization system; i.e. a system in which positions in space outside the body are defined by their distance and direction from the observer." The caudate nucleus contains or is contained in a system in which potential orienting movements of the head and eyes constitute the code for spatial localization. The internal representation of each point P in space is the set of motor programs which turn the head and the eyes such that P is in focus, given a particular position of the body.

Barbeau (1972) lists the following functions for the striatum: "1. Feedback, "filter" function in postural tone control mechanisms. 2. "Set" function in the state of preparedness for movement. 3. "Trigger" function in the initiation of movements. 4. "Strategy" programming in some mental functions. 5. Feedback integration and modulation of autonomic and neurohumoral homeostasis."

Divac (1972, 1977, and in press): "The neostriatum is the first link in one of two parallel channels through which the neocortex affects motor mechanisms. By virtue of topographic organization of its neocortical afferents, NS appears as a cluster of units each performing some, possibly the same, operations on the input arriving from respective neocortical systems. Figuratively speaking, NS can be considered as a part of the system which translates cognition into action."

Cools (1973, 1975, and in Van den Bercken and Cools, 1979): "The neostriatum forms part of a system in which incoming signals, representing the actual situation, are compared with previously established links or expectations between components of behavioural programs; responsible either for the simultaneous composition of behavioural patterns or for the temporal combination of behavioural responses. Normal activation of the neostriatum produces a breakdown of the behavioural program and enables the organism to establish new programs according to available information. ..... this process is active at both the motor level and the mental level."

Frigyesi (1975a, b): Excitatory output of the caudate nucleus reaches the dorsal thalamus via the substantia nigra; there it exerts control over the activities in the cerebellocortico-spinal projection system, by transforming sensory (proprioceptive) input patterns to those of motor coordination (system response). "The caudate removes the animal from the tyranny of the proprioception; and .... the substantia nigra mediated this effect to the sensorimotor system proper." The "Caudate does not initiate movement; it participates in the integration of those corticopetal activities which do." "It should not be inferred ..... that scaffolding motor activities is the sole function of the basal ganglia. The basal ganglia, in conjunction with other systems, are involved in a wide range of activities, from proper adaptation to the environment, affective display, motor symbolism, and communication to mimicry. Equally important is that the caudate has been shown to be able to interfere with all aspects of memory formation, acquisition, consolidation, retention and recall. The caudate not only aids the animal to distinguish signal from noise, but also in signal detection, determination of channel summation and integration."

Buchwald (in Buchwald et al., 1975): "The search for any single concept (i.e. motor function, sensory function, attention) to express the role of the basal ganglia in regulating behavior ..... may not be meaningful." (in Soltysik et al., 1975): "The basal ganglia serve as neural substrates for the regulation of cognitive and response sets.....". (in Neafsey et al., 1978): "..... There is a preparatory "set" period before a movement and the neural substrate of this "set" appears to include the basal

ganglia, VL-VA, and medial "motor" cortex in the cat....." "The basal ganglia participate in enabling and sequencing of movements rather than in directly causing them to occur....."

Villablanca (1975, see also: Villablanca et al., 1976a, b, c; Olmstead et al., 1976): "The basal ganglia are not only concerned with motor functions ..... The basal ganglia operate at a high level of CNS integration and appear to be involved in two main types of, generally speaking, sensorimotor functions: a) the control of some of the organism-environment inter-relationships, both at a behavioral and neurological level , a context of regulating the balance between approach and avoidance reaction ..... b) the preparation or "setting up" of the organism for performance of both complex motor responses (response set), and of tasks requiring a high level of cognition (cognitive set) ..... High level integration means here that ..... the basal ganglia control most probably operates upon performances not triggered reflexy, directly or indirectly, from the periphery but originated internally either "volitionally" or generated by symbolic, e.g. verbal, instructions. The above functions appear to be accomplished by means of a modulatory action upon afferent signals arriving into the telencephalon and triggering efferent activities through forbrain output structures, particularly the neocortex ..... The literature on the effect of lesions and stimulation experiments ..... suggest that the basal ganglia are also involved in mental processes ..... Finally, the basal ganglia may also be involved in other bodily homeostatic functions including hormonal, autonomic and neurotransmitter regulatory mechanisms....."

Webster (1975) argues for "a wider role for the corpus striatum than that conceived of in the classical sense of "motor" ....." and for "the involvement of the striatum in complex central functions in close association with the cerebral cortex....." From the available data "it is still possible to maintain that the basal ganglia are part of the motor system. But some of the current experimental evidence indicates that this involvement with motor performance is at a level of complexity that brings into relief the problems attendant upon distinguishing a category known as "motor activity" from another to be called "behaviour"..

That a motor act, be it of a "simple" or of a "complex behavioural" nature, is or may be under sensory control other than somatosensory is a commonplace. Such control obviously includes the initiation and cessation of an act. Assuming that control is exercised at least in part upon the cortico-spinal systems, by what pathways does such information reach the motor cortices? In view of the extensive origin of its neocortical input, the multimodal nature of its unit discharges, and its large efferent discharge to the precentral cortex ..... the corpus striatum is an obvious candidate for this role....."

Denny-Brown (1976) states with respect to the basal ganglia "that the natural function of these structures is the facilitation of movement. The manner in which this function is performed has so far eluded all investigation." The main deficit after striatal lesions "would appear to be (the absence of) the activating "set" or "pump primer" for a certain act, the preparation of the mechanism preparatory to a motor performance oriented to the environment." ..... "The basal ganglia have all the aspects of a "clearing house" that accumulates samples of ongoing cortical projected activity, and, on a competitive basis, can facilitate any one and suppress all others."

Teuber (1976): "It is apparent, however, that in animal and man, basal ganglia functions include complex perceptual and cognitive aspects of behavior, and require a reconsideration of the much too restricted view of these structures....." "It seems to us that an important feature of basal ganglia function, although differently expressed through different subsystems, is neither purely motor nor purely sensory, but sensorimotor in the strictest sense, involving an information flow that goes from systems previously called "extrapyramidal motor" to both central receptor and effector regions. Such signals, we postulate, preset those other regions for the consequences of concurrent or impending actions. The proposal would entail an entire class of unorthodox discharges, not only from sensory to motor, in the traditional Sherringtonian direction, but essentially from motor to sensory, preparing sensory systems for the kind of input that will be produced by the execution of various efferent actions.

We have called these unorthodox loops "corollary" and "proleptic" discharges, respectively, depending on whether they accompany outflow signals or precede them in time."

Hassler (1978) considers the striatum "as a part of the non-specific thalamocortical activating system, which we prefer to call trunco-thalamic system....." "The diffusely projecting trunco-thalamic nuclei, as for example the intralaminar, para-fascicular and center median, do not send an appreciable number of their afferent fibers directly to cortical areas, but rather to the parts of the striatum and pallidum ..... The different cortical fields, however, are able to moderate the electrical activity of the striatum through a well organized system of direct cortico-striatal neurons ..... The non-specific cortico-petal impulses are integrated with one another in the striatum ....." Efferent pathways from the caudate nucleus and the globus pallidus then head for the thalamus again, terminating in the VA- and the VL-nucleus. Hassler identifies the pallidum as "an activating centre for locomotion and turning attention, as though fascinated, towards an object or event appearing from the contralateral side. In contrast, the function of the putamen (and the caudate nucleus) is revealed as mostly inhibitory regulation of spontaneous or stimulus-induced motor, ipsiversive locomotor or psychomotor and attentional activities and adaptation of the intentional actions to the actual situation ..... Each site of putamen tissue is able to enhance alertness, emotional reaction and intentional action to one outer event, and at the same time, to cause all other environmental stimuli and simultaneous intentional actions to fade and dim....." In the best German tradition of detailed localization the synapses and transmitters constituting the mechanism of the functions described are then specified.

Ward (1968): "There has been general agreement that these structures (the basal ganglia) play a role in motor activity, and the growing body of experimental and clinical data has provided some minor sophistication to such statements. Unfortunately, our knowledge of the detailed function of these interrelated structures is incomplete so that a meaningful synthesis is not possible."

Laursen (1963): "The function of the corpus striatum is on a high level of integration."

COMMENT

It will be clear from the previous section that the ideas concerning the role of the caudate nucleus in behaviour are beset with much obscurity. The list of quotations does not, by itself, very much to promote our knowledge on caudate nucleus functioning; nevertheless, as it stands, it gives a fair impression of the state of the art in brain-behaviour research; in fact, a similar anthology could easily be made for any other brain structure currently under study, e.g. the hippocampus or the locus coeruleus. Some common themes may be found in several of the proposed accounts of striatal functioning; the intersection of several sets of opinions however does not necessarily convey validity to its content. Some of the accounts on the caudate nucleus are so comprehensive as to prompt the question why the brain should have other parts as well.

The main problem with much of the brain-behaviour work is the lack of adequate theory on behavioural phenomena and psychological processes. It is often attempted to outline how the brain subserves some behavioural function before a clear picture has emerged of what the brain precisely is supposed to do or what kind of function it should implement. It is not the purpose of this chapter to discuss the predicament of brain-behaviour research in general. The point to be made is that the literature on the caudate nucleus does not offer much guidance for experimental research. The work to be reported upon in the next two chapters is therefore motivated by other, slightly pragmatic considerations. Firstly, the caudate nucleus has been an object of investigation at the psychopharmacological section of the Nijmegen Laboratory of Pharmacology for years. Both neurobiological and neurobehavioural work has been performed (Cools, 1973; Cools et al., 1975a; Cools et al., 1977). From that work a concept of striatal functioning has been emerging that is sufficiently well-defined to be studied in neurobehavioural experiments. Secondly, most neurobehavioural work on the caudate

nucleus has been done with single subjects, under rather restricted conditions of testing. The development of techniques for chemical telestimulation (Cools et al., 1975b, 1978) made it possible to study the effects of caudate nucleus treatment in freely moving and interacting animals, which is particularly useful for social species like Java-monkeys. Therefore it was decided to investigate the hypothesis that the caudate nucleus is involved in the sequential organization of behaviour, particularly in the relationship between internal and external control, or intra-individual and extra-individual constraints. Since no particular task or test was to be used, the notions of internal and external control were translated in terms of properties of the interaction sequences that constituted the observed data.

CHAPTER 10

INJECTIONS OF CHOLINERGIC DRUGS INTO THE CAUDATE NUCLEUS OF JAVA-MONKEYS: EFFECTS ON THE SEQUENTIAL STRUCTURE OF BEHAVIOUR

In the previous chapter it was argued that acetylcholine is a transmitter of interneurons of the caudate nucleus. Consequently, cholinergic activity must have a central role in the intrinsic operation of the neostriatum and, accordingly, in the function of this nucleus in behaviour. It has been suggested that neostriatal cholinergic mechanisms are involved in the regulation of motor functions (DeFeudis, 1974; McDowell and Barbeau, 1974; Waser, 1975). Application of the cholinergic agent carbachol into the caudate nucleus elicits motor disturbances such as tremor, dyskinesia and even seizures (Connor et al., 1966a, b; Murphey and Dill, 1972). Using rhesus monkeys in a primate restraining chair, Cools was able to reproduce these findings at a dose of 10 μg of carbachol injected bilaterally into the head of the caudate nucleus (Cools et al., 1975a). This dose however, appeared uneffective in freely moving monkeys, when the injection was given by means of telestimulation. The present study was therefore designed to acquire further information on the selective role of the intrinsic cholinergic neurons of the caudate nucleus in behaviour. The activity of these neurons was manipulated by local injections of cholinergic agents (carbachol and atropine) in freely moving and interacting Java-monkeys (Macaca fascicularis). Specific questions concerning the behavioural aspects to be studied were related to a hypothesis on the function of the caudate nucleus, based on the available neurobehavioural literature (referred to in the previous chapter) and on previous experiments. The neostriatum is thought to be involved in the

process of selecting subsequent behaviour by comparing information concerning the environment with internal objectives (Cools, 1973). Accordingly, the present study treated the sequential structure of behaviour as the dependent variable. Ongoing behaviour was interpreted as determined by two factors: execution of individual programmes and reaction to environmental demands, formalized in correlations between intra-individual and inter-individual behaviour transitions.

EXPERIMENTAL METHODS

Subjects

The monkeys in the experiments to be described were the same as those used in earlier studies (chapters 6 and 7). Six different combinations of three animals out of five were made. One monkey from each triad, the reference subject, received micro-injections of a drug into the caudate nucleus by means of telestimulation; the other two monkeys in the triad constitute the partners of the reference subject. The relevant monkeys and triads are identified in Table 10.1 (and Table 6.1). The behaviour of the reference monkey and its partners was observed during several sessions for each experimental condition (drug). The injections were given at the beginning of the sessions, which lasted one hour. Successive sessions were separated by at least one day without chemical stimulation. The number of sessions per drug for each triad is shown in Table 10.1.

Surgery

Before the experiments all the monkeys were equipped with a small container for holding the chemical telestimulation apparatus (chemistor). The necessary surgery was carried out in two stages, about two weeks apart. In both operations the animals were pretreated with ketamine hydrochloride (Ketalar^{R}, 10 mg/kg i.p.) and atropine sulphate (0.5 mg, i.m.) and placed in a stereotactic apparatus (Heimer and Lohman, 1975) under halothane anaesthesia and artificial respiration. In the first operation a circular plastic container with an external diameter of 43 mm was fixed

onto the skull by means of four to six small tapered screws and dental cement. In the second operation guide cannulas with external diameters of 0.4 mm and internal diameters of 0.25 mm were placed in the head of the caudate nucleus, at co-ordinates A 18.5, L 5.0 and H 14.0, selected from the atlas of Shanta et al. (1968). After surgery at least one week was allowed for recovery.

Chemistor and drugs

For each series of experiments the reference monkey was equipped with two chemistors for bilateral injections. One chemistor consisted of a reservoir containing a drug solution and was connected to an implanted cannula by means of a polyethylene tube. The drug was injected by the movement one step forwards of a plunger in the reservoir. The plunger itself was driven by a spring motor activated by an electromagnet, with the energy for the electromagnet provided by a condenser in the lid of the chemistor container; for details, see Cools et al., 1975b.

Before the experiments, the reservoirs and inner cannulas were sterilized and filled with the appropriate drug solution. The actual fixing and connection of the chemistor in the container attached to the head took only a few minutes and was done under light anaesthesia (ketamine hydrochloride, Ketalar^{R}, 10 mg/kg i.p.). Each chemistor contained about 27 μl of drug solution with a single injection taking 0.9 μl. The following drugs were used: carbamylcholine chloride (carbachol, Sigma), and atropine sulphate (dissolved in aqua dest.). The necessary concentration of carbachol was established experimentally in the following way. The chemistor was filled with carbachol at a concentration of 8 μg/0.9 μl or 10 μg/0.9 μl. In the first session one injection was given to the reference monkey, and in the next session two immediately successive injections were given, i.e. a dose of 16 μg in a volume of 1.8 μl and so on, until motor disturbances (dyskinesia and/or tremor) appeared. The actual experiments were carried out with a dose equal to half the threshold dose for motor disturbances, which proved to be 20 μg in 1.8 μl or 30 μg in 2.7 μl (Table 10.1). The concentration of atropine sulphate was established at 88 μg/0.9 μl (cf. Prado-Alcala et al., 1972; Cools et al., 1975a) and the volume injected equal to that for carbachol,

TABLE 10.1

Composition of triads; number of sessions per drug-condition; and threshold dose to cause motor disturbances in the reference monkey

number triad	triad composition	reference monkey	number of sessions control	carbachol	atropine	first threshold	second threshold
1	1 3 4	1	5	5	5	40 μg (4.5 μl)	40 μg (3.6 μl)
2	1 3 5	1	5	5	5		
3	2 3 4	2	4	5	5	60 μg (5.4 μl)	60 μg (5.4 μl)
4	2 3 5	2	5	5	4		
5	1 3 4	4	5	5	4	40 μg (3.6 μl)	50 μg (4.5 μl)
6	2 3 4	4	5	5	5		

The monkeys are the same as those in Table 6.1

i.e. 1.8 μl or 2.7 μl. In the control condition only 2.7 μl of aqua dest. was injected. As it is known that the levels of ACh and its enzymes are subject to diurnal oscillation (Friedman and Walker, 1968; Hanin et al., 1970) all the experimental sessions took place between 8.30 and 10.30 a.m.

Chemical telestimulation

The procedure for chemical telestimulation required that the monkeys be housed in a special cage during the experiments. The cage (2 x 3 x 2 m) was constructed from formica covered wooden panels, placed inside a Faraday cabin, and surrounded by an aerial system in three orthogonal dimensions. The establishment of an electromagnetic field through the aerials for a number of seconds induced energy in a receiving coil and condenser in the lid of the chemistor container. The chemistor was actually triggered by the switching off of the power field; for details, see Cools et al., 1978.

Analysis of data

The behaviour of the monkeys was observed and recorded according to the methods described in chapters 2 and 3. The basic data consisted of frequencies of behaviour and of combinations of behaviours such as: the preceding and subsequent behaviour of the reference subject (= intra-individual transition), or of the preceding behaviour of a partner and subsequent behaviour of the reference subject (= inter-individual transition). The frequency distributions were analysed by means of the information-theoretical statistics for variability and association, described in chapter 4.

In order to determine the effects of cholinergic stimulation of the caudate nucleus on behaviour in more detail, with particular reference to the kind of behaviour transitions involved, two additional analyses were performed. Firstly, all combinations of the current behaviour of the reference subjects and the preceding acts of the reference subjects and their partners were sorted according to the presence or absence of orientation, as outlined in chapter 7.

Four types of behavioural interaction could be defined, corresponding to the following conditions of orientation:

1) both the reference subject and his partner were orientated towards each other, that is, were showing behavioural signs of orientation (= physical contact, or locomotion, postures or expressions directed at an identifiable partner);
2) only the partner orientated at the reference subject;
3) only the reference subject orientated at the partner;
4) no mutual orientation was present at all.

In chapter 7 it was found that communication as defined by partial cross-covariability did not coincide with communication as defined by the presence of behavioural orientation: even when monkeys did not show overt orientation at each other, the current behaviour of the reference monkey was constrained to a considerable degree by the preceding behaviour of its partner; similarly, in the presence of mutual orientation a high amount of autocovariability was found. At the same time however, the distinction of the four orientation conditions as defined above appeared to have some intrinsic meaning, as the amount of partial auto- and cross-covariability in each condition differed significantly. It might be of interest therefore, to investigate this dissociation between two aspects of communication (or even two kinds of communication) covered by cross-covariability and behavioural orientation respectively, further. We selected the conditions of mutual orientation and of no orientation, as being the most extreme cases, and measured the partial auto- and cross-covariability in each condition after injections of carbachol or atropine into the caudate nucleus.

The second additional analysis established a differentiation between continuation and change in ongoing behaviour in the reference subject. When the stimulated monkey continued its ongoing behaviour after a behaviour change in its partner, this was classified as a continuation-transition. A change-transition was recorded when the reference monkey did indeed change its behaviour. The partial covariability measures were first computed from the original protocols, which contained both types of transition, and then from a subset of the protocols, which contained change-only transitions.

Histology

After completion of the experiments the monkeys were sacrificed under anaesthesia (pentobarbital) and perfused transcardially (saline and subsequently formaldehyde 10%). The brains were removed stereotactically, immersed in 4% formaldehyde and embedded in paraffin wax. Some slices of brain were made along the paths of the guide cannulas. The injection sites were located with the help of Shanta's atlas (Shanta et al., 1968). The sites were discovered to be confined to the head of the caudate nucleus, as shown in Fig. 10.1. There was some variation in the A-P direction: site no. 2 was most prominent at about A 20.5 and site no. 6 was located best at A 16.0.

RESULTS

The behaviour variability of the reference monkey after intracaudate application of various cholinergic drugs was computed over the frequency distributions of 49 different behavioural states, accounting for 85% of the total observation time. The results are shown in Fig. 10.2. The maximum variability was $\log_2 49 = 5.61$ bits. The average actual variability for the triads in the control condition was 4.07 bits (standard deviation (sd) = 0.19 bits). Injection of the cholinergic agent carbachol into the caudate nucleus caused an increase in variability: H = 4.77 bits (sd = 0.20 bits), significantly different from the control value at $p \leqslant 0.025$, according to Wilcoxon's matched-pairs signed-rank test. Monkeys treated with carbachol apparently dis-

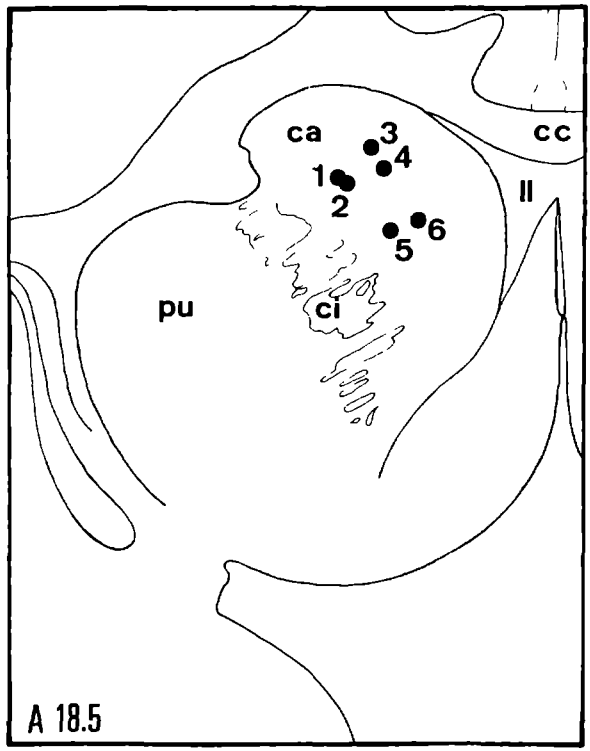


Fig. 10.1

Location of the injection sites projected onto the coronal plane A 18.5 of Shanta's atlas (Shanta et al., 1968).
ca = nucleus caudatus; ci = capsula interna; pu = putamen; cc = corpus callosum, II = ventriculus lateralis.
Odd numbers refer to sites in the right hemisphere and even numbers to sites in the left hemisphere.

tribute their time more randomly or more evenly over the available activities. The variability of behaviour after an injection of the anticholinergic drug atropine was not significantly changed: H = 3.93 bits (sd = 0.06 bits; probability of differing from control value: $p > 0.05$ according to Wilcoxon's test). The average total sequential covariability, i.e. the proportion of the variability of ongoing behaviour due to correlation with the immediately preceding behaviours of the reference subject and its

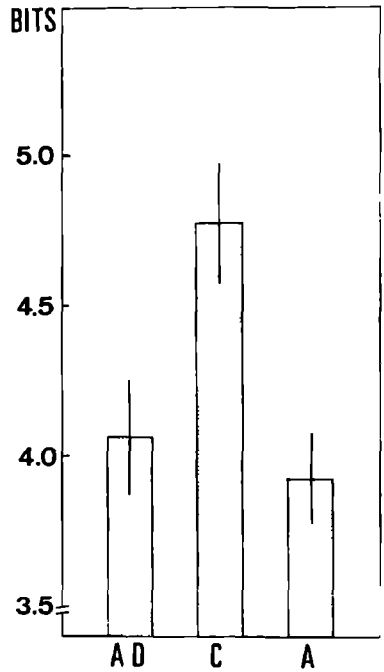


Fig. 10.2

Mean total variability of behaviour (plus range, ± 1 sd) of the reference monkeys in the six triads after intracaudate injections of aqua dest. (= AD), carbachol (= C) or atropine (= A)

partner, is shown in Fig. 10.3. In the carbachol-condition the total sequential covariability was slightly, but consistently, higher: a rise from 77% to 84% on average ($0.025 \leqslant p \leqslant 0.05$ by Wilcoxon's test). In the atropine-condition the total sequential covariability was not significantly different from the control value. Taken together, the increase in absolute variability and in total sequential covariability indicates that after intracaudate injections of carbachol monkeys display behavioural bouts

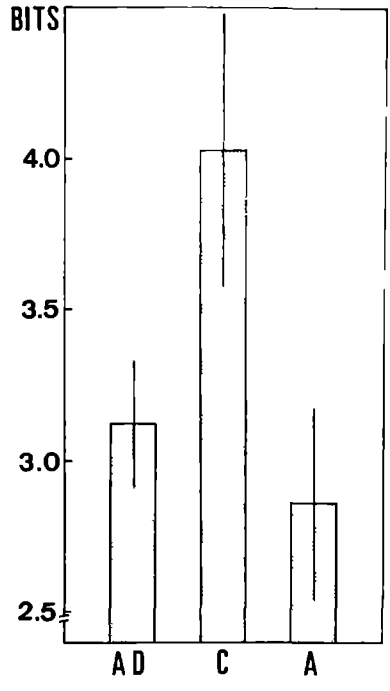


Fig. 10.3

Mean total sequential covariability (plus range, ± 1 sd) of the reference monkeys in the six triads after intracaudate injections of aqua dest. (= AD), carbachol (= C) or atropine (= A)

of a wider variety than usual.

The next step was to assess the separate contributions of the preceding behaviour of the stimulated monkey and that of its partners to the selection of the current behaviour of the stimulated monkey. Figure 10.4 shows the average partial auto- and cross-covariabilities of the reference monkeys under each experimental condition, as a proportion of the total sequential

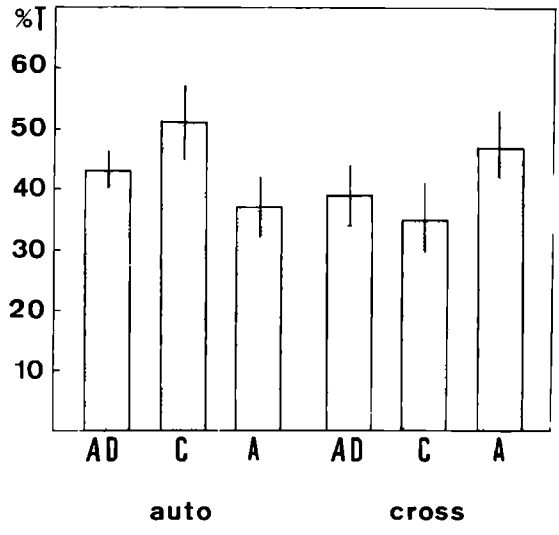


Fig. 10.4

Mean partial autocovariability (= auto) and partial cross-covariability (= cross) of the reference monkeys in the six triads after intracaudate injections of aqua dest. (D), carbachol (= C) or atropine (= A) as proportion of the total sequential covariability (plus range, ± sd)

covariability. After an intracaudate injection of carbachol the normal balance between auto- and cross-covariability changed. The correlation between the current behaviour of a reference monkey and its own preceding behaviour increased on average from 43% to 51% in the six triads ($p \leq 0.025$ by Wilcoxon's test). Response to the preceding behaviour of the partners remained unaffected ($p > 0.05$, Wilcoxon's test). Atropine, on the other hand, did change the balance, primarily by affecting the partial cross-covariability. After intracaudate application of atropine the inter-individual correlation increased significantly from

39% to 47% on average ($p \leq 0.025$, Wilcoxon's test). The intra-individual sequential constraint, as measured by the partial autocovariability, was lowered slightly by atropine, from 43% to 37% ($0.025 \leq p \leq 0.05$ by Wilcoxon's test).

The constraints imposed on ongoing behaviour were further characterized by investigating several types of behaviour sequences. Firstly, the partial auto- and cross-covariabilities were computed for mutually orientated interactions and for non-orientated interactions, and the results shown in Table 10.2.

TABLE 10.2

Variability measures for the reference subject's orientated and non-orientated interaction after intracaudate injection of various cholinergic drugs

		Aqua dest.	Carbachol	Atropine
Orientation	H	4.14	4.35	4.09
	T	3.12	3.57	3.46
	a	20	24	21
	c	59	55	70
No orientation	H	3.95	4.73	4.14
	T	2.78	3.19	3.06
	a	48	62	53
	c	44	34	39

H = total individual variability (in bits)
T = total sequential covariability (in bits)
a and c = partial auto- and cross-covariability (as proportion of T)

Carbachol and atropine had different effects on the balance between intra- and inter-individual constraints in both kinds of interaction. When there was no explicit orientation between

individuals, carbachol significantly increased the autocovariability, from 48% to 62% ($p < 0.01$, according to the test described in chapter 8). The cross-covariability decreased significantly from 44% to 34%. In the case of non-orientated behaviour transitions, atropine did not have a significant effect on either the intra- or inter-individual correlation. When the reference subject and its partner were involved in mutually orientated interaction, carbachol had no effect on intra- or inter-individual constraints. Atropine, however, significantly increased the cross-covariability in the case of orientated behaviour, from 59% to 70%, without affecting the autocovariability.

Secondly, the partial auto- and cross-covariability measures were computed for transitions involving a continuation of behaviour in the stimulated monkey and for those involving a change of behaviour. The results are shown in Table 10.3.

TABLE 10.3

Variability measures for behaviour transitions in the reference monkey involving continuation and change of behaviour after intracaudate injection of various cholinergic drugs

		Aqua dest.	Carbachol	Atropine
Continuation	H	3.77	4.12	3.83
	T	2.60	2.85	2.36
	a	52	67	45
	c	24	21	33
Change	H	4.29	4.98	4.41
	T	3.26	3.57	3.13
	a	31	36	28
	c	47	38	58

Abbreviations are the same as in Table 10.2

Once again carbachol and atropine had different effects on the balance between intra- and inter-individual constraints in different situations. When the reference monkey continued its behaviour (after a change in its partner's behaviour), the auto-covariability was significantly increased by carbachol, from 52% to 67%; the cross-covariability was however not significantly affected ($p > 0.10$ and $p > 0.20$ respectively according to our test of chapter 8). Atropine tended to reduce the autocovariability ($0.025 < p < 0.05$) and significantly to increase the cross-covariability in the case of continuation, from 24% to 33% ($p < 0.02$ by our test). When the stimulated monkey actually changed its behaviour, the contribution of its own preceding behaviour was not affected by carbachol; the auto-covariability of 36% was not significantly different from the control value of 31%; the cross-covariability decreased from 47% to 38% ($p < 0.02$). In the case of change, atropine did not affect the intra-individual constraints, but significantly increased the inter-individual constraints, from 47% to 58% ($p < 0.01$).

DISCUSSION

Methodological remarks on chemical telestimulation

Repeated use of permanently implanted cannulae can endanger the stability of the effects: histological changes may render the injection site ineffective or tolerance may develop for a given drug. In order to check this possibility, the threshold experiments with injections of carbachol were repeated for each reference monkey. The period between the first and second series of threshold experiments varied from five to eight months and the intervening history of chemical stimulation differed for each monkey. From the last column in Table 10.1 it is clear that there was no consistent change in the thresholds, suggesting that the effectiveness of the injection site remained virtually unchanged.

Great care was taken in these experiments to avoid disturbing the morphology of overt behaviour. In fact, this was the reason for first determining the threshold doses for motor disturbances which have been reported to result from cholinergic stimulation

of the neostriatum. The effective dose for motor disturbances in the present study (Table 10.1) seems to be quite high compared to the doses used by other investigators. Connor et al. (1966a, b), for example, injected 7 μg in 8 μl into unanaesthetized, but severely restrained cats, and observed marked tremors. Hull et al. (1967) used "high" doses of 4 to 10 μg in less than 4 μl in freely moving cats equipped with leads for electrical recording and stimulation; they observed autonomic responses and contralateral turning and circling but no tremor until 45-60 minutes after the injection. Stevens et al. (1961) report that an estimated amount of 25 μg to 50 μg of crystalline carbachol resulted in contralateral circling and akinesia. More relevant are the experiments of Murphey (1972) with individual squirrel monkeys in small cages. He observed a complex hyperkinetic choreiform syndrome after injection of 3.75 μg in 3.75 μl. The syndrome consisted of ataxia, loss of balance, followed by tremor and dyskinesia, leading eventually to convulsions. In rhesus monkeys held in a primate restraining chair Cools (1975a) observed a similar syndrome for a dose of 10 μg carbachol in 10 μl. Several possibilities may be considered in attempting to account for these differences. Firstly, our injection sites may not be exactly homologous to those in the cited studies and consequently, the dose would have to be high in order to reach the effective sites by diffusion. Although this possibility cannot be completely rejected, there are two objections. One is that it implies a rather confined area within the caudate nucleus from which motor disturbances can be obtained, which does not seem very likely. The other is that the observed latency times ranged from 6 to 18 minutes, which is not very different from the latency times reported by others (Murphey and Dill (1972): 8.8 mins; Connor et al. (1966a, b): 9-21 mins). Secondly, an explanation of the high dose in our case could be found in the permanent implantation of cannulae connected continuously with a reservoir containing the drug solution. The drug might diffuse from the cannula into brain tissue, thereby establishing a concentration gradient in the cannula. In such a case the actual amount of drug injected with a certain volume of solution would be less than the amount calcu-

lated from the original concentration. This explanation seems however to be ruled out by the fact that with several monkeys motor disturbances could be reproduced with the same dose but with different time intervals between the placing of the filled reservoir and the actual injection. Although the available data is not quite consistent, it suggests two other factors that might be relevant: the volume injected and the degree of restraint imposed on the animals by the experimental situation. Injections of greater volume which pervade larger areas of the brain (Myers, 1974) may be effective with lower doses, and the threshold for overt motor disturbances may be lowered under conditions of stress. The validity of this explanation must await empirical verification of its hypotheses. In any case, in view of the relative size of the caudate nucleus in the squirrel monkey and in the Java-monkey at comparable co-ordinates, it is clear that a Java-monkey requires a higher dose to activate an identical proportion of tissue. Finally, it should be mentioned that we did not observe signs of cholinergic kindling that have been reported to occur in rats after a number of daily injections of carbachol into the neostriatum (Vosu and Wise, 1974).

In the foregoing discussion the motor disturbances caused by carbachol were strongly emphasized because they represent immediately observable effects and can therefore be used for methodological checking. However, we were not primarily interested in pathological changes in the morphology of behaviour but were looking for effects representing psychological changes manifest in the structure of behaviour. The fact that such changes are indeed present brings up an important point (irrespective of their interpretation): it may be very misleading to wait for directly observable behavioural effects resulting from interference with the brain (e.g. chemical or electrical stimulation, or lesion); subtle changes in the structure of individual behaviour and of social interaction may occur long before clear-cut overt responses develop. It may not be justified to identify a certain brain area as involved in, for instance, motor or aggressive behaviour, in cases where the intensity of stimulation or the dose of a drug is increased until such effects become

apparent. Other effects, at lower intensities or doses, may be easily overlooked. A continuum of manipulation, e.g. electrical or chemical stimulating with varying intensities or doses, need not correlate with only one continuum of gradually emerging effects.

Intracaudate cholinergic mechanisms and behaviour

In order to interpret the results satisfactorily, it must be realized that Fig. 10.4 and Tables 10.2 and 10.3 represent the same data broken down in different ways, and thus analysed by different aspects. The dimensions for this breakdown ("presence/absence of orientation" and "continuation/change of behaviour") cannot be regarded as independent variables in the causation of the particular covariability values observed. They merely serve to identify classes of behavioural interactions that were possibly associated with particular changes in the intra- and inter-individual constraints expressed in the covariability measures. The only independent variable in this study was the state of the cholinergic neurons in the caudate nucleus, as affected by injections of carbachol, atropine or aqua dest. Several aspects of ongoing behaviour were however clearly affected by this treatment and the findings are summarized here:

1. Carbachol increased the overall variability of behaviour.
2. Carbachol increased the total sequential constraints on ongoing behaviour, arising from the immediately preceding acts of the stimulated monkey and its partner. The preceding behaviour of the stimulated monkey and that of its partner contributed to the selection of the subsequent behaviour of the reference monkey to a different degree under each of the experimental conditions.
3. Carbachol increased the intra-individual constraints but at the same time slightly decreased the inter-individual constraints; atropine however increased the inter-individual constraints. These changes in the relative weight of intra- and inter-individual constraints in ongoing behaviour were not the same for different types of behavioural interaction.
4. The increase in autocovariability caused by carbachol was most prominent when the stimulated monkey was not involved in orien-

tated behaviour and when it was maintaining its current behaviour. The decrease in cross-covariability caused by carbachol occurred in non-orientated behaviour and in changes of behaviour.

5. The increase in cross-covariability caused by atropine was associated with orientated behaviour and with changes in as well as continuations of ongoing behaviour. In the latter case atropine also tended to decrease the autocovariability.

It is tempting to conclude from 4 that carbachol decreases the inter-individual constraints in the case of non-orientated changes in behaviour; and from 5 that atropine increases the cross-covariability in the case of orientated continuation of and orientated changes in behaviour. However, such conclusions are not justified, because the auto- and cross-covariabilities were not computed for the combined dimensions "presence/absence of orientation" and "continuation/change of behaviour". As it stands, the effects of carbachol and atropine on the behaviour of monkeys freely moving and interacting with other monkeys are rather complex. Nevertheless, it is possible to summarize the findings in the following statement: carbachol increases the intra-individual sequential constraints, and decreases the inter-individual sequential constraints. Atropine's prime effect is to increase the inter-individual constraints.

These findings appear to be in line with a number of neuro-behavioural findings on the caudate nucleus, especially from lesion studies. Lesions of the neostriatum in rats, cats and monkeys consistently produce a deficit in alternation behaviour, appearing as response perseveration (Bättig et al., 1960, 1962; Chorover and Gross, 1963; Rosvold and Delgado, 1963; Gross and Chorover, 1965; Butlers and Rosvold, 1968; Rosvold, 1968; Goldman and Rosvold, 1972; Divac, 1972a; Winocur, 1974; Öberg and Divac, 1975). Monkeys with lesions of the caudate nucleus fail to adapt to spatial displacement of visual inputs by prismatic spectacles (Bossom, 1965). Such monkeys also have impediments in the performance of visuomotor tracking (Bowen, 1969). These effects are not due to impairment of perceptual abilities since visual discrimination tasks are not affected (Divac, 1972b; Gold-

man and Rosvold, 1972). Similar effects are seen in human patients with lesions of the basal ganglia when set to perform tasks requiring perceptually guided control of behaviour (Bowen, 1976; Flowers, 1978). In cats not subjected to specific cognitive tasks, ablation of the caudate nucleus results in compulsory approach ("stimulus binding") and hyperreactivity (Villablanca et al., 1975, 1976; Olmstead et al., 1976). These effects can be interpreted as having a disturbed integration of internally and externally generated control in common, in particular, a reduction in the flexibility of response to changes in the external situation as manifested by response perseverance, stimulus binding and tracking failure. In the present study no restrictions were imposed on the monkey's behaviour, i.e. no tasks or tests were set to concentrate on particular behavioural functions. It can be assumed that freely moving and interacting monkeys function at a high level of psychological organization, recruiting virtually any process aimed at in specific test situations. Consequently, the effect of experimenting on the caudate nucleus ought to reflect a close similarity to the effects found under specific experimental conditions. This is indeed the case. Blocking the intrinsic cholinergic mechanism of the caudate nucleus by atropine can be taken as functionally equivalent to ablation. The increased cross-covariability which occurs after injections of atropine indicates an increase in correlation between the current behaviour of the stimulated monkey and the preceding behaviour of its partners, or, equivalently, a reduction in response-variability; the stimulated monkey reacts to its partners in a more predictable way, using fewer alternatives. Equally, if the anticholinergic drug atropine causes a functional blocking in the caudate nucleus and at the same time a reduced flexibility in behaviour, the opposite effect should be expected when the cholinergic neurons in the caudate nucleus are activated by carbachol. This is indeed what happens. The variability in response to the behaviour of others is increased by injections of carbachol, as shown by the reduced cross-covariability. At the same time, the internal control of ongoing behaviour is less variable as is apparent from the increased autocovariability. The caudate nucleus seems therefore to be involved in effecting

an integration between internal and external control and at the same time in establishing flexibility in the progression of ongoing behaviour. That some high-level integrating process affecting the balance between auto- and cross-covariability is involved can be deduced from the fact that the factors are not affected separately. Carbachol increases the autocovariability and also decreases the cross-covariability; atropine slightly decreases the autocovariability and also increases the cross-covariability. It can therefore be concluded that a cholinergic mechanism in the caudate nucleus is concerned with both factors simultaneously; it may be particularly involved in the establishment of the relative priorities of internal and external constraints on programming ongoing behaviour.

INJECTION OF CHOLINERGIC DRUGS INTO THE CAUDATE NUCLEUS AND THE AMYGDALA OF JAVA-MONKEYS: EFFECTS ON DIFFERENT CATEGORIES OF BEHAVIOUR

In order to provide a proper context of interpretation for the findings reported in the previous chapter some additional data is needed. Two questions in particular must be answered: 1) Does cholinergic stimulation of the caudate nucleus indeed affect the sequential structure of behaviour rather than some other aspect of behavioural organization which then in turn might bring about changes in sequential constraints? 2) Are the effects of cholinergic activation of the caudate nucleus characteristic for that nucleus or can they be elicited from other brain structures as well? In this chapter it is attempted to evaluate the effects of carbachol and atropine more directly, in terms of what a stimulated monkey is doing or of what kind of behaviour he engages in; changes in the frequencies of behaviours belonging to different ethologically defined categories are presumed to be indicative for the function of a brain structure in behaviour. The effects of cholinergic drugs applied to the caudate nucleus are compared with the effects of the same drugs applied to the nucleus amygdalae (nucleus basalis lateralis). The latter is chosen as a control structure because it has been shown to be sensitive to treatment by cholinergics (Grossman, 1963; Hernández Péon et al., 1967; Girgis, 1972; Ben-Ari et al., 1977) and because it has been suggested to be involved in particular classes of behaviour (Goddard, 1969; Kaada, 1972; Kling, 1972; Allikmets, 1974; Nagy and Decsi, 1976; Zagrodka and Fonberg, 1978).

EXPERIMENTAL METHODS

The experimental methods are the same as described in the previous chapter, except for the following additions.

Subjects, surgery and drugs

Data on the effects of cholinergic treatment of the caudate nucleus on frequencies of behaviour were obtained by the experiments described in the previous chapter. Data on the amygdala were taken from experiments performed earlier with three different (naive) subjects. Two pairs of monkeys were used, one male-male pair and one male-female pair (one male was common to both pairs). Each monkey was equipped with cannulae in the amygdala, bilaterally at coordinates A 18.5, L 5.0 and H 14.0 selected from Shanta's atlas (1968). The members in each pair received four to five applications of the drugs carbamylcholine chloride (carbachol, 20 μg in 1.8 μl) and atropine sulphate (50 μg in 1.8 μl) or the solvent, aqua dest. (1.8 μl).

Observation and analysis of behaviour

Protocols obtained under identical experimental conditions were pooled and frequency distributions were subsequently made of the behaviours of the stimulated monkey; these served as the main dependent variable for evaluating the effects of the drug. As described below, 25 behaviour patterns were specially selected for the analysis. The patterns could be grouped into categories corresponding with ethologically defined motivational systems. The rationale for the assumption of such systems and some techniques for identifying them have been outlined by Hinde (1970, chapters 15 and 25). The categories of behaviour used in this report are based on a number of ethological studies on the behaviour of Java-monkeys (Thompson, 1969; Angst, 1974; De Waal et al., 1976; Deag, 1977). Not all the elements of the complete behaviour repertoire of Java-monkeys were used since an element had to occur frequently enough for statistical analysis. The 25 behaviours included accounted for 40% to 60% of the total number of behaviour patterns which occurred during the observations and were broken down into five categories. Category I comprised the

following behaviours: yawning, scratching (slowly or quickly), self-grooming, eating (including picking food up and cleaning it) and drinking (licking or suckling). This category was considered to represent maintenance behaviour. In the second category, II, a range of sexual behaviour was counted: presenting, anogentical inspecting, mounting, copulating and grasping or reaching backward (by the female during copulation). Category III consisted of positive social or affiliative behaviours: lip-smacking, inviting for grooming, touching, grooming and huddling. Category IV consisted of threats and aggression: fixating, open mouth threat, bobbing head or shoulders, lunging and chasing. Finally category V represented behaviours expressing submission and fear: gaze aversion, grinning, shrinking, crouching and fleeing.

Statistical methods

To assess the effect of the injected drugs on behaviour in general the frequencies of each behaviour after injection of the solvens were compared with the frequencies of behaviour after injection of the drugs carbachol or atropine. The frequency distribution for aqua dest. was considered to represent the frequencies expected for the drug-conditions, when the null hypothesis of no effect would prevail. The differences were tested by means of the chi-square test (Siegel, 1956). To answer the question whether the drugs affect different categories of behaviour differently, the following approach was used. Firstly, the change in the frequency of each behaviour under the experimental condition was quantified. Three measures were considered, each incorporating a different aspect of change.

a) The amount of change was measured by the absolute value of the difference between the relative frequency of each behaviour under the control and experimental conditions: $|p_{i(c)} - p_{i(e)}|$, where p_i is the relative frequency of behaviour i in both conditions.
b) The degree of change was also taken into account, since it might be argued that the absolute difference between $p_{i(c)}$ and $p_{i(e)}$ should be evaluated according to the baseline value present under control-conditions; the same amount of change

should be given more weight in the case of a low initial value. The degree of change was measured as: $(|p_{1(c)} - p_{1(e)}|)/p_{1(c)}$.

c) The third aspect of change is its direction: the difference should be signed instead of being taken absolutely; this is expressed by the measure $(p_{1(c)} - p_{1(e)})/p_{1(c)}$. For each of these indices a Kruskal-Wallis one-way analysis-of-variance test was carried out (Siegel, 1956), to check whether the categories of behaviour, I-V, differed in respect of the changes brought about by the drug. Such is the case when the rank-orders of the measures of change for all behaviours are not equally distributed over the categories. The test-statistic was evaluated by a chi-square approximation.

Histology

The brains of the amygdala monkeys were treated in the same way as the brains of the caudate monkeys (chapter 10). The injection sites were located by visual inspection and found to be well within the target area, i.e. the nucleus basalis lateralis of the amygdala and the head of the caudate nucleus. In one of the amygdala monkeys one of the cannulae (left) appeared to be located somewhat in the direction of the lateral part of the amygdala.

RESULTS

Caudate nucleus

The distributions of the relative frequencies of the behaviours belonging to the categories I - V after injections of carbachol or atropine are shown in Fig. 11.1 (and in the appendix). The frequency distributions under each experimental condition were tested against that of the control condition and were found to be significantly different: $\chi^2 = 2333.42$, df = 24 and $p < .001$ for carbachol, and $\chi^2 = 1089.47$, df = 24 and $p < .001$ for atropine.

Turning to the relationship of these changes with the behavioural categories I - V, Fig. 11.2 shows the effects of carbachol on the amount of change in each category. The absolute values of

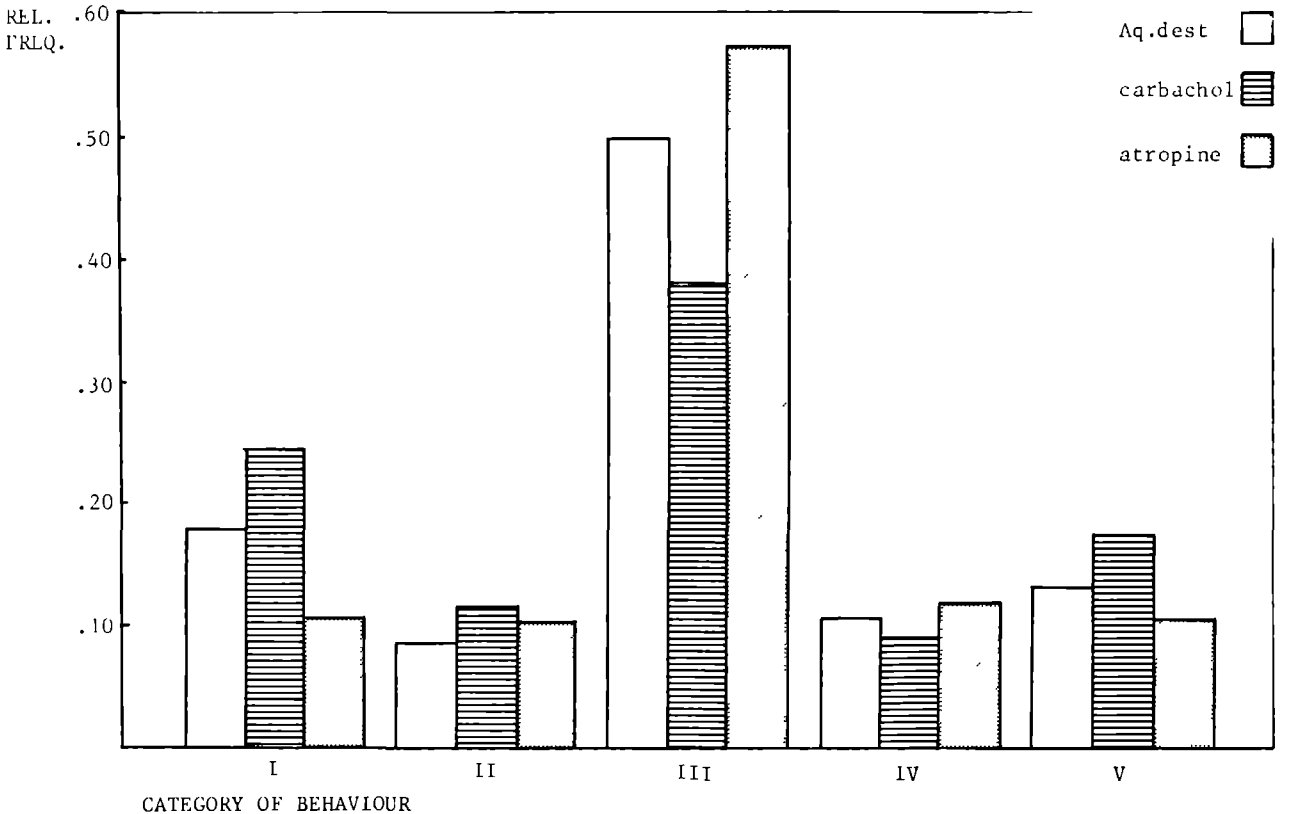


Fig. 11.1

Relative frequencies of the behaviour patterns of the categories I - V, after injections of carbachol, atropine or aqua dest. into the caudate nucleus of Java-monkeys

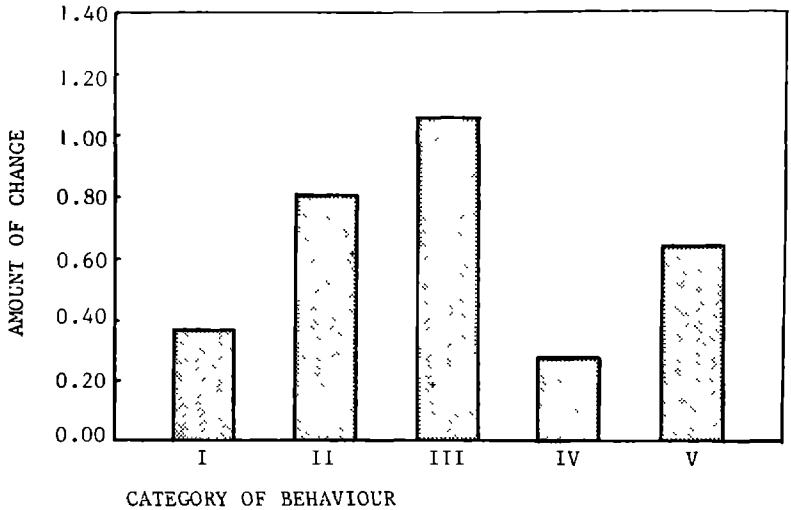


Fig. 11.2

Amount of change in the relative frequencies of occurrence of the behaviours in categories I - V after injections of carbachol into the caudate nucleus

the difference between the relative frequencies under the experimental and control conditions were summed over the five behaviour patterns in each category. Similarly, Fig. 10.3 shows the amount of change brought about by atropine. The results of the tests on the various aspects of change are given in Table 11.1. There was no difference in the way carbachol changed the behaviours category by category; the actual distribution of the amount, degree and direction of change over the various categories was well within the probability range for the null-hypothesis. Nor in the case of atropine was the change apparently restricted to any class of behaviour in particular. This result is somewhat marginal, especially with respect to the direction of change. However, the data appear to support the conclusion that no single category is exclusively affected by atropine: although in category III all behaviours increased in frequency, in three other

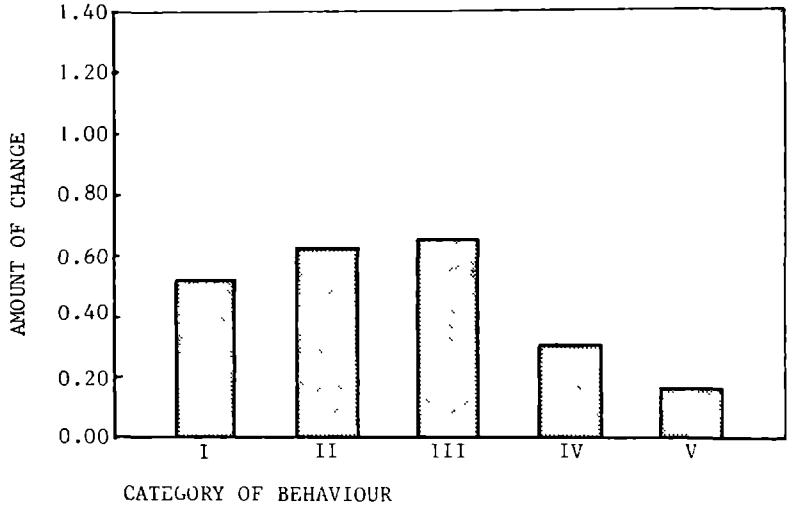


Fig. 11.3

Amount of change in occurrence of behaviours in categories I - V after injection of atropine into the caudate nucleus

TABLE 11.1

Evaluation of the changes in the occurence of behaviours of various categories after injection of carbachol or atropine into the caudate nucleus. Kruskal-Wallis's statistic (H) and associated levels of probability based on chi-square approximation (df = 4, in all cases) are given for the three aspects of change defined in the text.

change	carbachol vs control	atropine vs control
amount	H = 4.96 .20 < p < .30	H = 7.05 .05 < p < .10
degree	H = 3.57 .30 < p < .50	H = 8.06 .05 < p < .10
direction	H = 3.98 .30 < p < .50	H = 13.10 .02 < p < .05

categories (II, IV and V) some behaviours (eight in total) also showed increases. Increases and decreases are not therefore restricted to one class of behaviour (see also appendix).

Amygdala

Injections of carbachol into the basal nucleus of the amygdala also resulted in a changed frequency distribution of the various behaviours (Fig. 11.4 and appendix). When tested against the control observations, the frequency distribution for carbachol proved to be significantly different: $\chi^2 = 1197.99$, df = 24, $p < .001$. The distribution for atropine however, did not differ from that for aqua dest.: $\chi^2 = 36.02$, df = 24, $.10 < p < .20$. The absolute amount of change caused by carbachol and atropine in the basal nucleus for the various categories of behaviour is shown in Figs. 11.5 and 11.6. The results of a Kruskal-Wallis analysis-of-variance test for the various measures of change are presented in Table 11.2. Especially for carbachol, the degree and the direction of change are unevenly distributed over the categories I - V. Figs. 11.4 and 11.5 indicate clearly that categories IV and V are particularly affected, i.e. both aggressive and submissive behaviour occur much more frequently after injections of carbachol. However, this did not occur to a similar degree in each individual monkey. The increase in aggressive behaviour occurred mainly in the male-male pair, when the stimulated monkey was the dominant one. When the other male in this pair was stimulated, the result was mainly an increase in submissive behaviour. The same happened in the male-female pair, when the female was stimulated with carbachol. The changes caused by atropine in the basal nucleus do not appear to be significant.

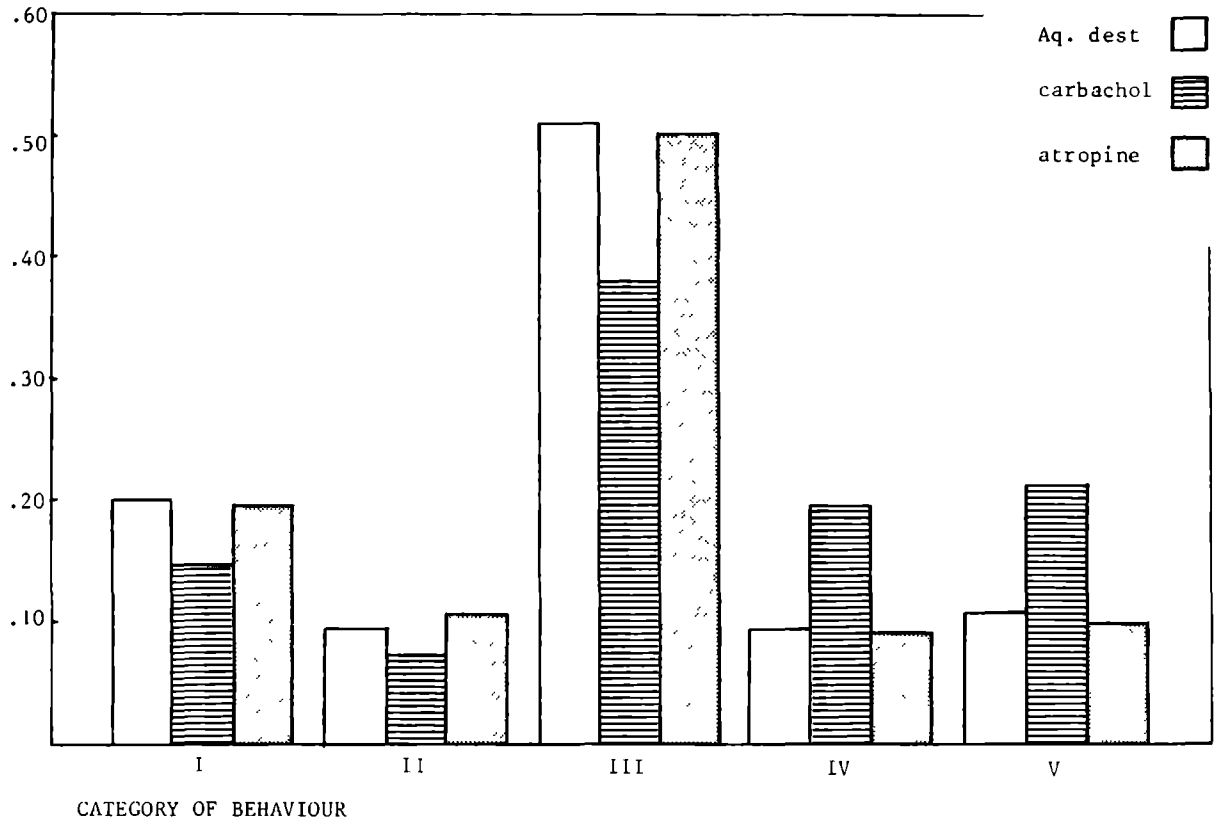


Fig. 11.4

Relative frequencies of the behaviours in the categories I - V, after injections of carbachol, atropine or aqua dest. into the nucleus basalis of the amygdala of Java-monkeys

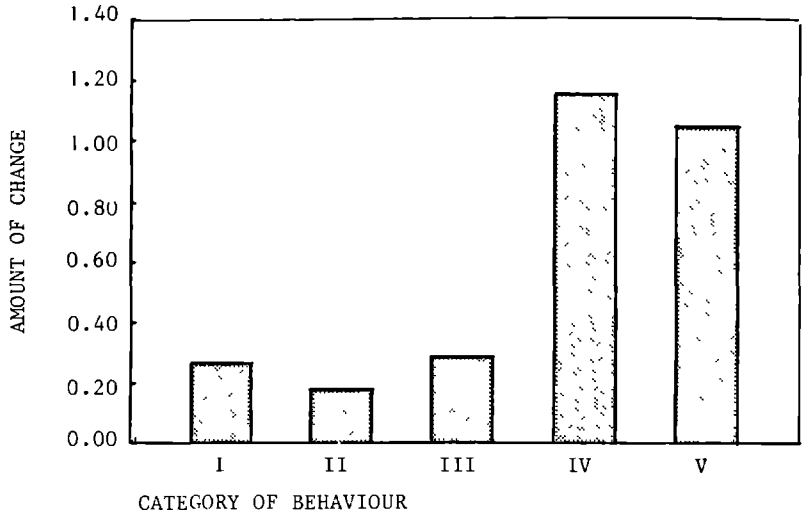


Fig. 11.5

Amount of change in occurrence of behaviours in categories I - V after injection of carbachol into the nucleus basalis of the amygdala

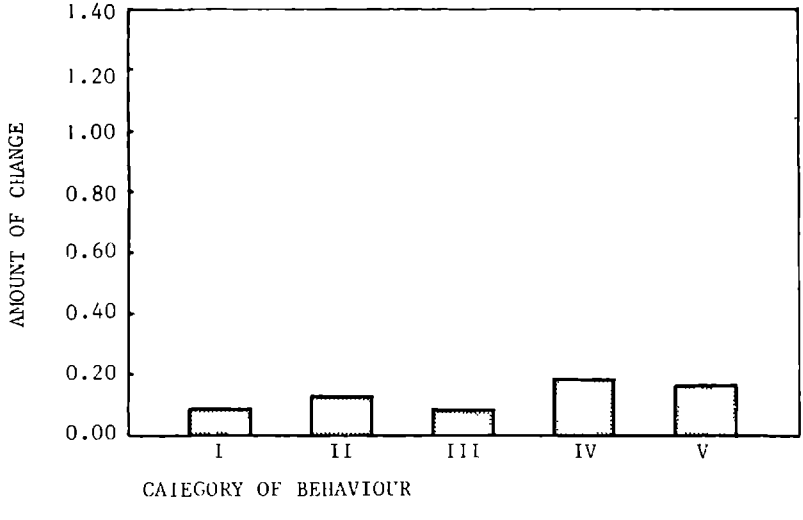


Fig. 11.6

Amount of change in occurrence of behaviours in categories I - V after injection of atropine into the basal nucleus of the amygdala

TABLE 11.2

Evaluation of the changes in the occurrence of behaviours in various categories after injection of carbachol or atropine into the basal nucleus of the amygdala. Kruskal-Wallis's statistic (H) and associated levels of probability based on chi-square approximation (df = 4) are given for the three aspects of change discussed in the text

change	carbachol vs control	atropine vs control
amount	H = 9.87 $.02 < p < .05$	H = 2.97 $.50 < p < .70$
degree	H = 17.84 $.01 < p < .001$	H = 5.49 $.20 < p < .30$
direction	H = 17.44 $.01 < p < .001$	H = 5.63 $.20 < p < .30$

DISCUSSION

The following comments are appropriate in respect of the effects of cholinergic treatment of the amygdala. We did not explicitly test for the factors sex and dominance, but the data suggests that dominance is a relevant parameter as far as the effect of carbachol is concerned; dominance relationships are important in the maintenance of a stable social structure in groups of monkeys (De Waal et al., 1976; Deag, 1977). The fact that both aggression and submission can increase after cholinergic stimulation of the amygdala seems to imply that this nucleus is involved in the control of factors determining social relationships (Kling, 1972; Kling and Steklis, 1976). Formulated in this general manner, our findings are consistent with other data on the role of the amygdala (Bellazi, 1972; Kaada, 1972; Allikmets, 1974; Zagrodka and Fonberg, 1978).

The fact that atropine had no effect at all when applied to the amygdala is somewhat puzzling, but two explanations are possible. Firstly, when cholinergic activation of the basal nucleus

results mainly in an increase in agonistic behaviours, then the opposite effect would be a decrease in such behaviours. However, when the baseline level is already low, a decrease beyond the minimum level would scarcely be noticeable statistically. The second possible reason for the absence of any effect from atropine would be that sub-threshold doses were applied. In the present experiments we did not go beyond a dose of 50 μg of atropine applied in two steps; each stimulation released a volume of 0.9 μl. If larger volumes had been used, it would have been difficult to restrict the drug to the selected area of the amygdala.

The results of the experiments in stimulating the caudate nucleus can be summarized by stating that cholinergic activation or blocking of this nucleus has an effect that is not restricted to the particular motivation categories of behaviour used in our experiments. This means that ethologically defined unity at the behavioural level does not necessarily convey functional unity at the neurobiological level. In the previous chapter it was shown that cholinergic stimulation of the caudate nucleus changes the sequential structure of ongoing behaviour: carbachol increased the dependency between the preceding and the subsequent behaviour of the stimulated monkey, while atropine's main effect was to increase the dependency between the current behaviour of the stimulated monkey and that of other monkeys. Taken together, the findings imply that the caudate nucleus is not concerned with the control of a particular class of behaviour but rather with a more general function in the programming of ongoing behaviour. Specifically, it has been proposed that the caudate nucleus combines and integrates both information concerning the actual external situation (i.e. information on what other animals are doing) and information stored internally, representing goals or purposes of the individual. The net effect of this function is to provide the flexibility and continuity in ongoing behaviour, which are necessary both to maintain behavioural programmes, once initiated and also, at the same time, to cope with incidental variations in the external situation.

APPENDIX

Frequencies of 25 behaviour patterns of Java-monkeys after injections of carbachol (= C), atropine (=A) or the solvent aqua dest. (= AD) into the caudate nucleus

behaviour pattern	AD	C	A
yawning	205	331	59
scratching	422	475	165
self-grooming	472	428	191
eating	437	434	356
drinking	246	446	108
presenting	103	246	177
inspecting	162	108	262
mounting	205	485	164
copulating	157	95	79
grasping backward	75	40	139
lip-smacking	137	213	160
inviting grooming	191	170	184
touching	20	99	70
grooming	1538	1105	1820
huddling	2488	1682	2629
fixating	280	229	229
open mouth	253	217	289
bobbing	55	89	74
lunging	129	117	191
chasing	177	118	201
gaze aversion	225	230	168
grinning	109	341	102
shrinking	191	320	189
crouching	403	437	252
fleeing	184	194	152

Frequencies of 25 behaviour patterns of Java-monkeys after injections of carbachol (= C), atropine (= A) or the solvent aqua dest. (= AD) into the basolateral nucleus of the amygdala

behaviour pattern	AD	C	A
yawning	56	59	66
scratching	186	201	203
self-grooming	123	76	132
eating	171	165	209
drinking	75	81	106
presenting	60	63	79
inspecting	51	46	77
mounting	101	95	138
copulating	44	56	60
grasping backward	36	45	46
lip-smacking	52	42	59
inviting grooming	81	83	86
touching	17	28	17
grooming	566	496	696
huddling	838	892	1020
fixating	82	241	98
open mouth	67	184	62
bobbing	22	81	33
lunging	44	116	46
chasing	71	167	102
gaze aversion	53	132	73
grinning	32	102	47
shrinking	63	152	72
crouching	109	310	114
fleeing	61	166	91

CHAPTER 12

SUMMARY AND CONCLUSIONS

The work that this thesis reports on is concerned with the analysis of social interaction (in Java-monkeys) in the context of neuro-ethological research into the caudate nucleus of the brain. The general problem was how the effects of experimental manipulation of the brain (particularly the caudate nucleus) could be interpreted in terms of characteristics of ongoing behaviour (particularly its sequential structure). The content of this thesis can accordingly be divided into two parts: an ethological and data-analytical part (chapters 2-8), and a neurobehavioural part (chapters 9-11). The ethological part elaborates on the methodology of describing, observing and analysing social behaviour. The neurobehavioural part reports the changes in the behaviour of Java-monkeys caused by injections of cholinergic drugs into the caudate nucleus.

In chapter 2 the literature on the behaviour of Java-monkeys is briefly discussed and an inventory of the definitions used in subsequent chapters presented. Several comprehensive descriptions are available, based on different principles. Some authors, for example, have been defining behaviour patterns by enumerating a subset of one or more elements from a list of perceptual primitives corresponding to easily recognizable states of effector systems. It has been proposed, alternatively, to interpret the organism as a system of several independently varying components and to describe the behaviour of an animal as a vector variable. Both methods are illustrated in some detail and general problems associated with the construction of an ethogram are discussed, in particular the problem of representing simultaneous activities

in a consistent way. Finally, a method for describing behaviour by means of a simple generative syntax is suggested.

Chapter 3 discusses a system for observing, recording and protocolling ongoing behaviour. It is shown that current microprocessor technology can be profitably used in an interactive procedure for protocolling behaviour as recorded on videotapes. In our experiments behaviour was observed by means of two cameras; one provided a wide-angle survey of the whole cage; while the other could be remotely controlled and focused on a particular monkey under study. The behaviour, once recorded on videotapes, could be converted into protocols by the use of a minicomputer system. At the beginning of a session each monkey's initial state was entered, which consisted of codes for behaviour, location, and orientation to other monkeys; after this only changes in this state were entered, and codes that did not change were re-entered into the protocol by the program in the processor; the time code associated with each new state was also added automatically as soon as the videotape was stopped. The behaviour codes were entered via the keyboard of a video-terminal, in the form of literal strings; they were checked for syntactical and lexical errors by the processor and transformed into numerical codes. A new description of the state of each monkey in the group was added to the protocol as soon as one or more individuals changed their behaviour. As a consequence, the same behaviour state could occur repeatedly in one animal as a result of changes in other animals.

Chapter 4 develops a procedure for analysing interaction sequences that is analogous to an analysis-of-variance; it is formulated using information-theoretical statistics. The basic data in our experiments consisted of frequencies of behaviours and of combinations of behaviours, such as the preceding and subsequent behaviour of a reference monkey (intra-individual transitions), or the preceding behaviour of a partner and the subsequent behaviour of the reference subject (inter-individual transitions). The frequency distributions were characterized by means of informational statistics for variability and association. From the intra- and inter-individual transitions we determined the relative contributions of the preceding behaviour of the reference monkey,

and of its partners respectively, to the selection of the subsequent behaviour of the reference monkey. These contributions were called the (partial) autocovariability and the (partial) cross covariability. The cross-covariability is a conventional index in ethology for the amount of communication between animals. The auto- and cross-covariability represent the effects of the preceding behaviours (of the reference monkey and its partners) separately; together with the interaction covariability, representing the effect of the specific combination of the preceding behaviours, they constitute the total sequential covariability, i.e. the total amount of variability in the present behaviour of a reference monkey that can be attributed to the immediately preceding behaviours of the reference monkey and its partners. The larger the total sequential covariability, the smaller the residual variability, i.e. that part of the variability that does not depend upon the preceding behaviours. The residual variability can be taken as a measure of the goodness of fit of a model in which a monkey's current behaviour is considered to depend on its own and its partner's preceding behaviour.

In ethological research, several other information-statistical models for interaction sequences have been proposed, especially for quantifying inter-individual effects. These models are reviewed and discussed in chapter 5, and can be summarized as follows. Model I is primarily concerned with first-order inter individual behaviour transitions in alternating interaction sequences; it takes the behaviour of the partner as a predictor for the subsequent behaviour of the reference subject. Model II regards the inter-individual effects in social interaction as being extended over first- to third-order transitions; it uses three successive preceding behaviours of the partners as predictor variables. Model III interprets the correlation between simultaneously occurring behaviours of two individuals as a result of communication and breaks this correlation into two components to represent the contributions of the separate individuals. Finally, model IV is once again restricted to first order transitions, but takes both intra- and inter-individual transitions into account (it is the model outlined in chapter 4). Every model can be regarded as an attempt to explain the variabil-

ity of the current behaviour of a reference subject by relating it to preceding behaviours. The more appropriate the predictors selected in each model, the smaller the residual variability will be. In the discussion of the various models particular attention is paid to the danger of confusing the covariability components when the predictor variables are inadequately identified.

In chapter 6 the various models described in the preceding two chapters are compared empirically, by applying each of them in turn to the same set of data. The following residual variabilities were found: 58% for model I, 41% for model II, 72% for model III, and 23% for model IV. It is clear that a small residual variability is not primarily associated with a large number of predictor variables (third-order inter-individual transitions in model II instead of first-order ones in model I) but rather with the choice of the right set of predictors (both intra- and inter-individual transitions in model IV instead of only inter-individual transitions in model II).

Our model for quantifying intra- and inter-individual effects in social interaction was developed primarily in order to be able to compare behaviour sequences under various conditions of caudate nucleus stimulation. That it can be applied, however, to several other aspects of behaviour is demonstrated in chapter 7. One obvious aspect of behaviour is its orientation as manifested by bodily contact or by direction of locomotion or gesture, which presumably reflects an intention to communicate. Inter-individual transitions were sorted according to the presence or absence of orientation in the reference monkey and its partner, and the partial auto- and cross-covariability computed for each of the four resulting kinds of behavioural interaction. The result was that even in the absence of reciprocal orientation a considerable amount of cross-covariability was present, implying that the behaviour of a reference monkey is to a great extent determined by that of its partners in a way that does not entail overt orientation. On the other hand, in the case of explicit reciprocal orientation, a high degree of auto-covariability was present; this means that even explicit behavioural reactions to other animals still remain influenced by the reference subject's own

preceding behaviour: ongoing behaviour reflects continuous integration of intra- and inter-individual influences.

The auto- and covariability measures can also be applied to the description of group structure. Chapter 7 shows that the covariability measures can be interpreted as factors determining the dominance relationships between monkeys in small groups.

The analysis of interaction sequences elaborated in chapters 4-7 is a special case of the analysis of multivariate categorical data. Chapter 8 contains a discussion of the general computational and statistical problems involved.

In chapter 9 some recent findings on the neuroanatomy and neurochemistry of the caudate nucleus are presented. The functions of this nucleus in behaviour continues to be a matter of speculation. The various hypotheses currently maintained are mostly merely paraphrases of the general statement that the caudate nucleus, in view of its complicated neurobiology, must play some role in complex behavioural and psychological processes.

In chapter 10 one particular hypothesis was investigated: that the caudate nucleus is involved in programming ongoing behaviour by comparing information on the actual external situation and information on the desired or expected situation. The caudate nucleus of Java-monkeys was treated with the cholinergic drugs carbachol and atropine, respectively to mimick and block the activity of the neurotransmitter acetylcholine, which is known to be contained in striatal interneurons. Aqua destillata was used as the solvent and applied in the control condition. The drugs were administered by means of a device for chemical telestimulation, controlled by radio signals, a procedure which does not require restraint or handling of the animals. The behaviour of the monkeys, who lived in small groups of three animals, was observed and protocolled as described in chapter 3, and analysed by the model discussed in chapter 4. In the context of the hypothesis on the function of the caudate nucleus to be tested, the auto- and cross-covariabilities were interpreted as indices representing the influences of external and internal control in ongoing behaviour. The average values of the partial auto- and cross-covariabilities (as proportions of the total sequential covariability) were found to be 43% and 39% in the control con-

dition, 51% and 35% after carbachol, and 37% and 45% after atropine. Carbachol increased the intra-individual association between successive behaviours; atropine mainly enhanced the inter-individual constraints and at the same time slightly decreased the intra-individual constraints. The increase in autocovariability was particularly significant when the reference monkey continued its ongoing behaviour despite a change in the behaviour of one of its partners; the increase in cross-covariability mainly occurred in the case of an actual change in the reference subject's behaviour. Moreover, the autocovariability did not increase after carbachol when the behavioural interaction between the stimulated subject and its partners was characterized by explicit mutual orientation. In such cases however atropine was effective in increasing the cross-covariability. Chapter 10 also discusses some technical problems associated with chemical telestimulation.

In chapter 11 some additional analyses and experiments are described. To exclude the possibility that the findings of chapter 10 are a result of changes in just one class of behaviour or motivational system (in the ethological sense), the following analysis was performed. From the original ethogram 25 behaviours were selected, belonging to five different categories: I. maintenance behaviour; II. sexual behaviour; III. affiliative behaviour; IV. fear and submission, and V. threat and aggression. Frequency distribution for the 25 behaviours were obtained under several conditions: injections of aqua dest. (= control), carbachol, or atropine into the caudate nucleus or the amygdala (basolateral nucleus). In the case of caudate nucleus treatment the frequency distributions under carbachol and atropine were significantly different from the control distribution. In the case of the amygdala injections only the carbachol distribution was changed. Several aspects of change were considered: the absolute amount of change (= absolute difference between the control and experimental frequencies), the proportion of the change (with respect to the initial control value), and the direction of change (increase or decrease after treatment). For the caudate nucleus injections, there were no significant differences in any of these measures of change between the five

categories of behaviour. For the amygdala treatment, the category of agonistic behaviours (categories IV and V) were considerably changed (increased) by carbachol. These results appear to confirm that the caudate nucleus has a general function that is not restricted to the control of a particular class of behaviour. For the time being this function appears to be as follows. The caudate nucleus, particularly its cholinergic neurons, affect the flexibility of behaviour by setting the relative priority of internal and external control of ongoing behaviour as manifested by the strength of association in intra-individual behaviour transitions and in inter-individual behaviour transitions.

It will be evident that the work reported upon in this thesis represents only a fraction of what is needed to clarify fully the relationship between the caudate nucleus and behaviour. The combination of techniques for analysing data on social interaction and techniques for experimenting on the brain in freely moving monkeys should however prove to be a powerful research tool. It offers the possibility of relating behavioural effects, consequent upon local injections into brain structures such as the caudate nucleus, to human data on disturbed motor functions (e.g. in Parkinsonism) and complex psychological processes (e.g. in schizophrenia), both of which are thought to involve a pathology of the caudate nucleus.

Het onderwerp van dit proefschrift is de analyse van sociaal gedrag (bij Java apen) in de context van onderzoek naar de rol die het caudatus-gebied van de hersenen heeft in het gedrag. De algemene vraagstelling was hoe de gevolgen van experimentele ingrepen in de hersenen, met name in de caudatus-kern, geïnterpreteerd kunnen worden in termen van kenmerken van het voortgaande gedrag, met name de volgorde-structuur daarvan. De inhoud van dit proefschrift kan dan ook in twee stukken verdeeld worden: een ethologisch en data-analytisch deel (de hoofdstukken 2 t/m 8) en een neuro-ethologisch deel (de hoofdstukken 9 t/m 11). Het eerste deel gaat over methoden voor het beschrijven, observeren en analyseren van sociaal gedrag. Het neuro-ethologisch deel brengt verslag uit van de veranderingen die door injecties van cholinerge stoffen in de caudatus-kern van Java apen bewerkstelligd worden in hun gedrag.

Hoofdstuk 2 bevat een discussie van de literatuur over het gedrag van Java apen, alsmede een lijst van gedragsdefinities die in de volgende hoofdstukken gebruikt is. Er bestaan enkele uitgebreide gedragsbeschrijvingen die gebaseerd zijn op verschillende principes. Sommige auteurs hebben gedragspatronen gedefinieerd met behulp van een lijst van gedragselementen die bestaan uit gemakkelijk waarneembare toestanden van groepen spieren; een gedragspatroon bestaat uit een of meer van zulke elementaire toestanden. Een ander soort definities ontstaat wanneer men het organisme opvat als een systeem waarvan de componenten zich min of meer onafhankelijk van elkaar kunnen gedragen: het gedrag is dan een vector-variabele. Deze twee methoden worden tamelijk uitvoerig toegelicht en enkele algemene problemen die samenhangen met het opstellen van een ethogram komen ter sprake, met name het probleem van consistente weergave van gelijktijdige activiteiten. Tenslotte wordt betoogd dat een aantal problemen

ondervangen kunnen worden door het gedrag te beschrijven met behulp van een eenvoudig syntactisch schema voor basistoestanden en object-gerichte activiteiten.

Hoofdstuk 3 beschrijft een systeem voor het observeren, vastleggen en protocolleren van het voortgaande gedrag. De huidige microprocessors kunnen met vrucht gebruikt worden in een interactieve procedure voor het protocolleren van het gedrag, nadat dit opgenomen is met behulp van video-apparatuur. In onze experimenten werd het gedrag geobserveerd met behulp van twee camera's: één met een groothoek lens die de hele observatiekooi overzag en één waarmee individuele apen gevolgd konden worden door middel van afstandsbediening. Zodra de gedragingen op een videoband stonden, konden ze in een protocol gecodeerd worden met behulp van een minicomputer en een programma. Bij het begin van een experiment werd de aanvangstoestand van elke aap ingetikt, bestaande uit codes voor gedrag, plaats en oriëntatie; daarna werden alleen de veranderingen in die toestand genoteerd. De niet-veranderde codes werden, evenals het tijdstip van elke verandering, automatisch ingevoegd in het protocol. Het programma controleerde voorts de codes op lexicale en syntactische fouten.

In hoofdstuk 4 wordt een procedure voor de analyse van interactie-sequenties ontwikkeld en geformuleerd met behulp van statistische grootheden uit de informatie-theorie. De basisgegevens in de experimenten bestonden uit frequenties van gedragingen en van combinaties van gedragingen, zoals het voorafgaande en volgende gedrag van een referentie-aap (intra-individuele overgangen) of het voorafgaande gedrag van een partner en het volgende gedrag van de referentie-aap (inter-individuele overgangen). De frequentie verdelingen werden beschreven met behulp van informatiematen voor variabiliteit en associatie. Op basis van de intra- en inter-individuele overgangen werden de relatieve bijdragen bepaald van de voorafgaande gedragingen van de referentie-aap en zijn partner aan de keuze van het volgende gedrag van het referentie-dier. Deze bijdragen werden aangeduid als de (partiële) auto-covariabiliteit en de (partiële) kruis-covariabiliteit. De kruis-covariabiliteit is een gangbare index in de ethologie voor de hoeveelheid communicatie tussen twee dieren.

De partiële auto- en kruis-covariabiliteiten vertegenwoordigen de afzonderlijke invloed van de voorafgaande gedragingen van de referentie-aap en diens partner; samen met de interactie-covariabiliteit die staat voor de invloed van de specifieke combinatie van voorafgaande gedragingen, vormen ze de totale sequentiële covariabiliteit, ofwel de totale hoeveelheid variabiliteit in het lopende gedrag van de referentie-aap die kan worden toegeschreven aan de onmiddellijk voorafgaande gedragingen van dezelfde aap en diens partners. Hoe groter de totale sequentiële covariabiliteit, des te kleiner de residuele variabiliteit, die niet terug te voeren is op de voorafgaande gedragingen. De residuele variabiliteit geeft aan hoe goed het lopende gedrag verklaard kan worden op basis van voorafgaande gedragingen.

Er zijn in de ethologische literatuur verschillende andere informatie-statistische modellen voor interactie-sequenties voorgesteld, met name voor het kwantificeren van inter-individuele invloeden (communicatie). Deze modellen worden besproken in hoofdstuk 5 en kunnen in het kort als volgt worden weergegeven. Model I houdt zich vooral bezig met eerste-orde inter-individuele gedragsovergangen in alternerende interactie-sequenties; het neemt het voorafgaand gedrag van de partner als voorspeller voor het volgende gedrag van het referentie-dier. In model II worden de inter-individuele invloeden uitgestrekt tot over derde-orde overgangen: drie opeenvolgende gedragingen van de partners worden betrokken in de voorspelling van het gedrag van het referentie subject. Model III interpreteert de correlatie tussen het gelijktijdig optredende gedrag van twee individuen als een gevolg van communicatie en splitst deze correlatie op in componenten voor de afzonderlijke bijdrage van elk subject. Model IV tenslotte beperkt zich weer tot eerste-orde overgangen, maar beschouwt zowel intra- als inter-individuele overgangen (dit is het model uit hoofdstuk 4). Elk model kan gezien worden als een poging de variabiliteit van het lopende gedrag van een referentie-subject te verklaren door het te relateren aan voorafgaande gedragingen. Naarmate de keuze van voorspellers juister is, zal de residuele variabiliteit kleiner zijn. Bij de discussie van de verschillende modellen werd speciaal ingegaan op het gevaar van verwarring van de covariabiliteitstermen wanneer de voorspellers onvoldoende

duidelijk geïdentificeerd worden.

In hoofdstuk 6 worden de modellen uit de voorafgaande twee hoofdstukken empirisch vergeleken door ze toe te passen op eenzelfde gegevensbestand. De volgende residuele variabiliteiten werden gevonden: 58% voor model I, 41% voor model II, 72% voor model III en 23% voor model IV. Het is duidelijk dat een kleine residuele variabiliteit niet zozeer optreedt bij een groter aantal voorspellers (derde-orde inter-individuele overgangen in model II tegenover eerste-orde overgangen in model I), maar veeleer bij de juiste keuze van de voorspellers (zowel inter- als intra-individuele overgangen in model IV tegenover alleen inter-individuele overgangen in model II).

Het model van hoofdstuk 4 werd primair uitgewerkt om gedragssequenties te kunnen vergelijken onder verschillende condities van stimulatie van de caudatus-kern. Dat het ook gebruikt kan worden in een andere context wordt gedemonstreerd in hoofdstuk 7. Het blijkt dat communicatie tussen twee dieren voorzover gedefinieerd als kruis-covariabiliteit niet samenvalt met communicatie voorzover vastgesteld aan de hand van waarneembare wederzijdse oriëntatie tussen de dieren (in termen van de richting van houdingen en bewegingen). Inter-individuele gedragsovergangen werden gesorteerd naar de aan- en afwezigheid van oriëntatie. Ook bij afwezigheid van gedragsmatige oriëntatie werd een aanzienlijke hoeveelheid kruis-covariabiliteit gevonden. Dit betekent dat het gedrag van een referentie-aap in hoge mate bepaald wordt door het voorafgaande gedrag van zijn partners door een vorm van communicatie waarbij geen waarneembare oriëntatie optreedt. Anderzijds werd er in het geval van expliciete wederzijdse oriëntatie een hoge mate van auto-covariabiliteit gevonden, hetgeen inhoudt dat ook bij expliciet reageren op het gedrag van een ander dier het eigen voorafgaand gedrag een belangrijke rol blijft spelen: het voortgaande gedrag weerspiegelt een voortdurende integratie van van intra- en inter-individuele processen.

De auto- en kruis-covariabiliteitsmaten kunnen ook gebruikt worden bij de beschrijving van de structuur van een groep. Hoofdstuk 7 laat zien dat deze maten geïnterpreteerd kunnen worden als factoren die de dominantie verhoudingen bepalen tussen apen in kleine groepen.

De analyse van interactie-sequenties zoals uitgewerkt in de hoofdstukken 4 en 7 vormt een speciaal geval van de analyse van multivariate nominale data. Hoofdstuk 8 bevat een discussie van de algemene rekentechnische en statistische problemen die zich daarbij voordoen.

In hoofdstuk 9 worden enkele recente gegevens inzake de neuroanatomie en de neurochemie van de nucleus caudatus gepresenteerd. De functie van dit hersengebied blijft een onderwerp van speculatie. De onderscheiden hypothesen die momenteel opgeld doen komen meestal neer op een parafrasering van de algemene uitspraak dat de nucleus caudatus vanwege zijn neurobiologische complexiteit wel een rol zal hebben in complexe gedragsmatige en psychologische processen.

In hoofdstuk 10 werd één bepaalde hypothese nader onderzocht: de betrokkenheid van de caudatus bij het programmeren van het voortgaande gedrag, met name bij een proces waarin informatie over de feitelijke situatie in de buitenwereld vergeleken wordt met informatie over de verwachte of gewenste toestand. De caudatus-kern van Java apen werd behandeld met carbachol en atropine met de bedoeling de activiteit na te bootsen en te blokkeren van acetylcholine, dat als neurotransmitter werkzaam is in interneuronen van de caudatus. Aqua dest. werd gebruikt als oplosmiddel en afzonderlijk in de controle behandeling. De stoffen werden toegediend met behulp van een apparaatje voor chemische telestimulatie, dat werd bestuurd door radiosignalen; aldus hoefden de proefdieren niet onnodig gehinderd te worden. De apen leefden in kleine groepjes van drie dieren; hun gedragingen werden geobserveerd en geprotocolleerd zoals beschreven in hoofdstuk 3 en geanalyseerd volgens het model uit hoofdstuk 4. In de context van de vraagstelling inzake de functie van de caudatus-kern werden de auto- en kruis-covariabiliteiten geïnterpreteerd als maten voor de invloed van externe en interne sturing in het voortgaande gedrag. De gemiddelde waarden voor de partiële auto- en kruis-covariabiliteit (als percentage van de totale sequentiële covariabiliteit) bleken 43% en 39% in de controle conditie, 51% en 35% na carbachol en 37% en 45% na atropine. Carbachol deed de intra individuele associatie tussen opeenvolgende gedragingen toenemen; atropine verhoogde voornamelijk de inter-individuele inperkingen

en verlaagde tevens enigszins de intra-individuele inperkingen. De toename in auto-covariabiliteit was met name aanzienlijk wanneer de referentie-aap zijn gedrag voortzette ondanks een verandering in het gedrag van zijn partners; de toename in kruis-covariabiliteit trad vooral op in het geval van een feitelijke verandering bij het referentie-dier. Verder bleek de auto-covariabiliteit niet toe te nemen wanneer de gedragsinteractie tussen het gestimuleerde dier en zijn partners gekenmerkt werd door expliciete wederzijdse geöriënteerdheid. In die gevallen gaf atropine echter wel een verhoging in kruis-covariabiliteit. In hoofdstuk 10 worden ook enkele technische problemen die samenhangen met chemische telestimulatie besproken.

In hoofdstuk 11 worden enkele aanvullende analyses en experimenten beschreven. Deze waren er op gericht om enerzijds de mogelijkheid uit te sluiten dat de bevindingen van hoofdstuk 10 toe te schrijven zijn aan veranderingen in slechts één categorie van gedragingen of motivationeel systeem (in de ethologische zin) en anderzijds na te gaan in hoeverre de bevindingen kenmerkend zijn voor het onderzochte hersengebied (de caudatus). Uit het oorspronkelijke ethogram werden 25 gedragingen genomen, behorend tot vijf verschillende categorieën: I. verzorgingsgedrag, II. sexueel gedrag, III. positief contact gedrag, IV. angst en submissie, en V. dreiging en agressie. Frequentie verdelingen voor deze 25 gedragingen werden verkregen onder verschillende condities: injectie van aqua dest. (= controle conditie), carbachol of atropine in zowel de caudatus-kern als de amandel-kern (het basolaterale deel). Behandeling van de caudatus met carbachol en met atropine resulteerde in significante veranderingen in de frequenties van de gedragingen. In de amygdala had alleen carbachol enig effect. Verschillende aspecten van de veranderingen werden bestudeerd: de absolute hoeveelheid (= het absolute verschil tussen de frequenties in de controle en experimentele conditie), de relatieve hoeveelheid (= percentage verandering t.o.v. de initiële conditie) en de richting (toename of afname). Bij de caudatus behandelingen waren er geen verschillen in deze drie maten voor de vijf gedragscategorieën. Bij de amygdala behandeling was er met name in de categorieën van agonistische gedragingen (IV en V) een aanmerkelijke verandering (toename).

Deze resultaten lijken te bevestigen dat de caudatus-kern een algemene functie heeft die niet beperkt is tot de sturing van een speciale klasse van gedragingen. Deze functie lijkt voorlopig het best als volgt te kunnen worden omschreven. De nucleus caudatus, met name de cholinerge neuronen daarin, beïnvloeden de flexibiliteit van het gedrag door het instellen van de relatieve prioriteit van interne en externe controle over het voortgaande gedrag zoals deze tot uiting komt in de sterkte van de associatie in intra-individuele gedragsovergangen en in inter-individuele gedragsovergangen.

Het moge duidelijk zijn dat dit proefschrift slechts een fractie vertegenwoordigt van het werk dat nodig is om de relatie tussen de caudatus en het gedrag op te helderen. De combinatie van technieken voor de analyse van sociale interactie en voor experimenten met de hersenen van vrij bewegende apen zal echter een krachtig middel kunnen blijken te zijn. Zo'n combinatie biedt de mogelijkheid gedragseffecten veroorzaakt door locale injecties in hersengebieden zoals de caudatus-kern in verband te brengen met gegevens over verstoringen in de motoriek bij de mens (zoals in Parkinsonisme) en in complexe psychische processen (zoals in schizofrenie), die beide mede op een pathologie van de caudatus kern zouden berusten.

Adrianov, O.S. and Shugalev, N.P. (1978) Mechanisms of participation of caudate nuclei in the organization of conditioned motor reflexes. Neuroscience 3, 139-141.

Allikmets, L.H. (1974) Cholinergic mechanisms in aggressive behaviour. Med. Biol. 52, 19-30.

Altmann, J. (1974) Observational study of behavior: sampling methods. Behaviour 49, 227-267.

Altmann, S.A. (1962) Sociobiology of rhesus monkeys I: A field study of the sociobiology of rhesus monkeys, macaca mulatta. Ann. N.Y. Acad. Sci. 102, 338-435.

Altmann, S.A. (1965) Sociobiology of rhesus monkeys II: Stochastics of social communication. J. theor. Biol. 8, 490-522.

Altmann, S.A. (1967) The structure of primate social communication. In: Social Communication among Primates (S.A. Altmann, ed.). The University of Chicago Press, Chicago and London, pp. 325-362.

Altmann, S.A. and Altmann, J. (1977) On the analysis of rates of behaviour. Anim. Behav. 25, 364-372.

Angst, W. (1974) Das Ausdrucksverhalten des Javaneraffen Macaca fascicularis Raffles. Fortschritte der Verhaltensforschung, Heft 15. Beiheft zur Z. Tierpsychol. Verlag Paul Parey, Berlin and Hamburg.

Angst, W. (1975) Basic data and concepts on the social organization of Macaca fascicularis. In: Primate Behaviour, Developments in Field and Laboratory Research (L.A. Rosenbaum, ed.) Vol. 4. Academic Press, New York, pp. 325-388.

Aspey, W.P. (1977) INFO: a program for computing information theory measures of communication. Behav. Res. Meth. & Instrum. 9, 305-306.

Barbeau, A. (1972) Biology of the striatum. In: Biology and Brain Dysfunction (G.E. Gall, ed.) Vol. 2. Plenum Press, New York, pp. 33-350.

Barker, R.G. (1963) The stream of behavior as an empirical problem. In: The Stream of Behavior (R.G. Barker, ed.). Appleton, New York, pp. 1-22.

Bastian, J. (1965) Primate signalling systems and human languages. In: Primate Behavior: Field Studies of Monkeys and Apes (I. de Vore, ed.). Holt, Rinehart & Winston, New York, pp. 585-606.

Bättig, K., Rosvold, H.E. and Mishkin, M. (1960) Comparison of the effects of frontal and caudate lesions on delayed response and alternation in monkeys. J. comp. Physiol. Psychol. 53, 400-404.

Bättig, K., Rosvold, H.E. and Mishkin, M. (1962) Comparison of the effects of frontal and caudate lesions on discrimination learning in monkeys. J. comp. Physiol. Psychol. 55, 458-463.

Batton III, R.R., Jayaraman, A., Ruggiero, D. and Carpenter, M.E. (1977) Fastigial efferent projections in the monkey: an autoradiographic study. J. comp. Neurol. 174, 281-306.
Baylis, J.R. (1976) A quantitative study of long-term courtship II: a comparative study of the dynamics of courtship in two new world cichlid fishes. Behaviour 59, 117-161.
Belluzi, J.D. (1972) Long-lasting effects of cholinergic stimulation of the amygdaloid complex in the rat. J. comp. Physiol. Psychol. 80, 269-280.
Ben-Ari, Y., Zigmond, R.E., Shute, C.C.D. and Lewis, P.R. (1977) Regional distribution of choline acetyltransferase and acetylcholinesterase in the amygdaloid complex and stria terminalis system. Brain Res. 120, 435-445.
Bertrand, M. (1969) The behavioral repertoire of the stumptail macaque: a descriptive and comparative study. Biblotheca Primatologica Vol. II. Karger, Basel.
Bossom, J. (1965) The effect of brain lesions on prism-adaptation in monkeys. Psychon. Sci. 2, 45-46.
Bowen, F.P. (1969) Visuomotor deficits produced by cryogenic lesions of the caudate. Neuropsychologia 7, 59-65.
Bowen, F.P. (1976) Behavioural alterations in patients with basal ganglia lesions. In: The Basal Ganglia (M.D. Yahr, ed.). Raven Press, New York, pp. 169-177.
Bregman, A.S. (1977) Perception and behavior as composition of ideals. Cogn. Ps. 9, 250-292.
Broekkamp, C.L.E., van Dongen, P.A.M. and van Rossum, J.M. (1977) Neostriatal involvement in reinforcement and motivation. In: Psychobiology of the Striatum (A.R. Cools, A.H.M. Lohman and J.H.L. van den Bercken, eds.). North Holland Publishing Company, Amsterdam, pp. 61-72.
Broekstra, G. (1978) On the representation and identification of structure systems. Int. J. Systems Sci. 9, 1271-1293.
Brownstein, M.J., Mroz, E.A., Tappaz, M.L. and Leeman, S. (1977) On the origin of substance P and glutamic acid decarboxylase (GAD) in the substantia nigra. Brain Res. 135, 315-323.
Buchwald, N.A., Hull, C.D. and Levine, M.S. (1975) Neurophysiological and anatomical interrelationships of the basal ganglia. In: Brain Mechanisms in Mental Retardation (N.A. Buchwald and M.A. Brazier, eds.). Academic Press, New York, pp. 189-203.
Butcher, L.L. (1977) Nature and mechanisms of cholinergic-monoaminergic interactions in the brain. Life Sci. 21, 1207-1226.
Butcher, S G. and Butcher, L.L. (1974) Origin and modulation of acetylcholine activity in the neostriatum. Brain Res. 71, 167-171.
Butlers, N. and Rosvold, H.E. (1968) Effect of caudate and septal nuclei lesions on resistance to extinction and delayed alternation. J. comp. Physiol. Psychol. 65, 397-403.
Cane, V.R. (1978) On fitting low-order Markov chains to behaviour sequences. Anim. Behav. 26, 332-338.
Carpenter, C.R. (1969) Approaches to studies of the naturalistic communicative behavior in nonhuman primates. In: Approaches to Animal Communication, Approaches to Semiotics (T.A. Sebeok and A. Ramsay, eds.) Vol. 1. Mouton, Den Haag, pp. 41-70.

Carpenter, M.B. (1976) Anatomical organization of the corpus striatum and related nuclei. In: The Basal Ganglia (M.D. Yahr, ed.). Raven Press, New York, pp. 1-36.
Chamove, A.S. (1974) A new primate social behaviour category system. Primates 15, 85-99.
Char-Tung Lee, R. (1971) Application of information theory to select relevant variables. Math. Biosci. 11, 153-161.
Chatfield, C. (1970) Analysing sequences of behavioural events. J. theor. Biol. 29, 427-445.
Cheyney, D.L., Le Fevre, H.F. and Racagni, G. (1975) Choline acetyltransferase activity and mass fragmentographic measurement of acetylcholine in specific nuclei and tracks of rat brain. Neuropharmacology 14, 801-810.
Chevalier-Skolnikoff, S. (1973) Facial expression of emotion in nonhuman primates. In: Darwin and Facial Expression: A Century of Research in Review (P. Ekman, ed.). Academic Press, New York, pp. 11-89.
Chevalier-Skolnikoff, S. (1974) The ontogeny of communication in the stumptail macaque, Macaca Arctoides. In: Contributions to Primatology, Vol. 2. Karger, Basel.
Chorover, S. and Gross, C.G. (1963) Caudate nucleus lesions: behavioural effects in the rat. Science 141, 826.
Chow, T.A. (1977) A statistical investigation of the time sampling methods in studying primate behaviour. Primates 18, 555-563.
Conant, R.C. and Steinberg, J.B. (1973) Information exchanged in grasshopper interactions. Inform. Control 23, 221-233.
Condon, W.S. and Ogston, W.D. (1967) A segmentation of behaviour. J. Psychiat. Res. 5, 221-235.
Connor, J.D., Rossi, G.V. and Baker, W.W. (1966a) Analysis of the tremor induced by injection of cholinergic agents into the caudate nucleus. Int. J. Neuropharmacol. 5, 207-216.
Connor, J.D., Rossi, G.V. and Baker, W.W. (1966b) Characteristics of tremor in cats following injections of carbachol into the caudate nucleus. Exp. Neurol. 14, 371-382.
Conrad, M. (1977) Functional significance of biological variability. Bull. Math. Biol. 39, 139-156.
Cools, A.R. (1973) The Caudate Nucleus and Neurochemical Control of Behaviour. Ph.D. Thesis. Brakkenstein Press, Nijmegen.
Cools, A.R. (1975) An integrated theory of the aetiology of schizophrenia. In: On the Origin of Schizophrenic Psychoses (H.M. van Praag, ed.). De Erven Bohn BV, Amsterdam, pp. 58-80.
Cools, A.R., Hendriks, G. and Korten, J. (1975a) The acetylcholine-dopamine balance in the basal ganglia of rhesus monkeys and its role in dynamic, dystonic, dyskinetic and epileptoid motor activities. J. Neurotransm. 36, 91-105.
Cools, A.R., Lagerwey, C., Lambrechts, P. and van Rossum, J.M. (1975b) Chemistor: a reusable telestimulation device for direct chemical stimulation of the nonhuman primate brain in freely moving animals. Physiol. & Behav. 14, 229-233.
Cools, A.R. and van Rossum, J.M. (1976) Excitation-mediating and inhibition-mediating dopamine receptors: a new concept towards a better understanding of electrophysiological, biochemical, pharmacological, functional and clinical data. Psychopharmacologia (Berl.) 45, 245-254.

Cools, A.R. (1977) Basic considerations on the role of concertedly working dopaminergic, GABA-ergic, cholinergic and serotonergic mechanisms within the neostriatum and nucleus accumbens in locomotor activity, stereotyped gnawing, turning and dyskinetic activities. In: Cocaine and Other Stimulants (E.H. Ellinwood and M.M. Kilbey, eds.). Raven Press, New York, pp. 97-141.

Cools, A.R. and van den Bercken, J.H.L. (1977) Cerebral organization of behaviour and the neostriatal function. In: Psychobiology of the Striatum (A.R. Cools, A.H.M. Lohman and J.H.L. van den Bercken, eds.). North Holland Publishing Company, Amsterdam, pp. 119-140.

Cools, A.R., Lohman, A.H.M. and van den Bercken, J.H.L. (1977) Psychobiology of the Striatum. North Holland Publishing Company, Amsterdam.

Cools, A.R., Lambrechts, P. and van Bommel, J. (1978) Wireless power-supplying system for implanted electronic circuits in freely moving animals. Med. & Biol. Eng. & Comput. 16, 559-563.

Corsi-Cabrera, M., Grinberg-Zylberbaum, J. and Arditti, L.S. (1975) Caudate nucleus lesion selectively increases paradoxical sleep episodes in the rat. Physiol. Behav. 14, 7-11.

Cronholm, J.N. (1963) A general method of obtaining exact sampling probabilities of the Shannon-Wiener measure of information $\hat{H}$. Psychometrika 28, 405-413.

Dale, M.B., MacNaughton-Smith, P., Williams, W.T. and Lance, G.N. (1970) Numerical classification of sequences. Austr. Comp. J. 2, 9-13.

Deag, J.M. (1977) Aggression and submission in monkey societies. Anim. Behav. 25, 465-474.

De Feudis, F.V. (1974) Central Cholinergic Systems and Behaviour. Academic Press, London.

Delgado, R.R. and Delgado, J.M.R. (1962) An objective approach to measurement of behavior. Philos. Sci. 29, 253-268.

Denny-Brown, D. and Yanagisaw, N. (1976) The role of the basal ganglia in the initiation of movement. In: The Basal Ganglia (M.D. Yahr, ed.). Raven Press, New York, pp. 115-150.

De Waal, F.B.M., van Hooff, J.A.R.A.M. and Netto, W. (1976) An ethological analysis of types of agonistic interaction in a captive group of Java monkeys (Macaca fascicularis). Primates 17, 237-290.

Dickman, H.R. (1963) The perception of behavioral units. In: The Stream of Behavior (R.G. Barker, ed.). Appleton, New York, pp. 23-41.

DiFiglia, M., Pasik, T. and Pasik, P. (1978) A golgi study of afferent fibers in the neostriatum of monkeys. Brain Res. 152, 341-347.

Dingle, H. (1969) A statistical and information analysis of aggressive communication in the Mantis Shrimp gonadactylus bredini Manning. Anim. Behav. 17, 561-575.

Divac, I. (1972a) Neostriatum and functions of prefrontal cortex. Acta Neurobiol. Exp. 32, 461-477.

Divac, I. (1972b) Delayed alternation in cats with lesions of the prefrontal cortex and the caudate nucleus. Physiol. Behav. 8, 519-522.

Divac, I., Fonnum, F. and Storm-Mathisen, J. (1975) High affinity uptake of glutamate in terminals of corticostriatal axons. Nature 266, 377-38 .
Divac, I. (1977) Does the neostriatum operate as a functional entity? In: Psychobiology of the Striatum (A.R. Cools, A.H.M. Lohman and J.H.L. van den Bercken, eds.). North Holland Publishing Company, Amsterdam, pp. 21-30.
Divac, I., Markowitsch, H.J. and Pritzel, M. (1978) Behavioral and anatomical consequences of small intrastriatal injections of kainic acid in the rat. Brain Res. 151, 523-532.
Divac, I. (1979) Proceedings of the workshop "The Neostriatum", organized by the European Brain and Behaviour Society, April 16-20, 1978. Plenum Press, London, in press.
Dunbar, R.I.M. (1976) Some aspects of research design and their implications in the observational study of behaviour. Behaviour 58, 78-98.
Eibl-Eibesfeldt, I. (1970) Ethology, The Biology of Behavior. Holt, Rinehart & Winston, New York.
Fagen, R.M. and Goldman, R.N. (1977) Behavioural catalogue analysis methods. Anim. Behav. 25, 261-274.
Fagen, R.M. (1978a) Information measures: statistical confidence limits and inference. J. theor. Biol. 73, 61-79.
Fagen, R.M. (1978b) Repertoire analysis. In: Quantitative Ethology (P.W. Colgan, ed.). Wiley, New York, pp. 25-42.
Fhanér, S. (1966) Some comments in connection with Rozeboom's linear correlation theory. Psychometrika 31, 267-269.
Fienberg, S.E. (1972) On the use of Hansen-frequencies for estimating rates of behavior. Primates 13, 323-326.
Flowers, K. (1978) Some frequency response: characteristics of parkinsonism on pursuit tracking. Brain 101, 19-34.
Fonnum, F., Gottesfeld, Z. and Grofova, I. (1978) Distribution of glutamate decarboxylase, choline acetyltransferase and aromatic amino acid decarboxylase in the basal ganglia of normal and operated rats. Evidence for striatopallidal, striatoentopeduncular and striatonigral gabaergic fibres. Brain Res. 143, 125-138.
Frigyesi, T.L. (1975a) Structure-function relationships of the interconnections between the caudate nucleus, globus pallidus, substantia nigra and thalamus. In: Subcortical Mechanisms of Sensorimotor Activities (T.L. Frigyesi, ed.). Huber, Bern, pp. 13-46.
Frigyesi, T.L. (1975b) Basal ganglia - thalamus interface. In: Subcortical Mechanisms of Sensorimotor Activities (T.L. Frigyesi, ed.). Huber, Bern, pp. 251-288.
Friedman, A.H. and Walker, C.A. (1968) Circadian rhythms in rat midbrain and caudate nucleus: biogenic amine levels. J. Physiol. 197, 77-85.
Furuya, Y. (1965) Social organization of the crab-eating monkey. Primates 6, 285-336.
Garner, W.R. and McGill, W.J. (1956) The relation between information and variance analyses. Psychometrika 21, 219-228.
Garner, W.R. (1962) Uncertainty and Structure as Psychological Concepts. Wiley, New York.

Girgis, M. (1972) The distribution of acetylcholinesterase enzymes in the amygdala and its role in aggressive behavior. In: The Neurobiology of the Amygdala (B.E. Eleftheriou, ed.) Plenum Press, New York, pp. 283-294.
Goddard, G.V. (1969) Analysis of avoidance conditioning following cholinergic stimulation of amygdala in rats. J. comp. Physiol. Psychol. 68, 1-18.
Golani, I. (1973) Non-metric analysis of behavioral interaction sequences in captive jackals (Canis aureus L). Behaviour 46, 89-112.
Goldman, P.S. and Rosvold, H.E. (1972) The effects of selective caudate lesions in infant and juvenile rhesus monkeys. Brain Res. 43, 53-66.
Goldman, P.S. and Nauta, W.J.H. (1977) An intricately patterned prefrontocaudate projection in the rhesus monkey. J. comp. Neurol. 171, 369-386.
Goustard, M. (1961) La structure sociale d'une colonie de Macaca Irus. Ann. Sci. Nat. Zool. 3, 297-322.
Goustard, M. (1963) Introduction à l'étude de la communication vocale chez Macaca Irus. Ann. Sci. Nat. Zool. 5, 707-748.
Grofova, I. (1979) Extrinsic connections of the neostriatum. In: Proceedings of workshop "The Neostriatum", April 16-20, 1978 (I. Divac, ed.). Plenum Press, London, in press.
Gross, C.G., Chorover, S. and Cohen, S. (1965) Caudate, cortical, hippocampal and dorsal thalamus lesions in rats: alternation and Hebb-Williams maze performance. Neuropsychologia 3, 53-68.
Grossman, S.P. (1963) Chemically induced epileptiform seizures in the cat. Science 142, 409-411.
Guyenet, P., Euvrard, C., Javoy, F., Herbet, A. and Glowinski, J. (1977) Regional differences in the sensitivity of cholinergic neurons to dopaminergic drugs and quipazine in the rat striatum. Brain Res. 136, 487-500.
Hailman, J.P. (1977) Optical Signals. Indiana University Press, Bloomington.
Haldane, J.B.S. and Spurway, H. (1954) A statistical analysis of communication in "Apis mellifera" and a comparison with communication in other animals. Insectes Sociaux 1, 247-283.
Hanin, I., Massarelli, R. and Costa, G. (1970) Acetylcholine concentrations in rat brain: diurnal oscillation. Science 170, 341-342.
Hassler, R. (1978) Striatal control of locomotion, intentional actions and of integrating and perceptive activity. J. Neurol. Sci. 36, 187-224.
Hauske, G. and Neuburger, E. (1968) Gerichtete Informationsgrössen zur Analyse gekoppelter Verhaltensweisen. Kybernetik 4, 171-181.
Hayes-Roth, F. and Longabaugh, R. (1972) REACT: a tool for the analysis of complex transitional behavior matrices. Behav. Sci. 17, 384-394.
Hazlett, B.A. and Bossert, W.H. (1965) A statistical analysis of the aggressive communication systems of some hermit crabs. Anim. Behav. 13, 355-377.

Hazlett, B.A. and Estabrook, G.F. (1974a) Examination of agonistic behavior by character analysis I: the spider crab Microphyrs bicornutus. Behaviour 48, 131-144.
Hazlett, B.A. and Estabrook, G.F. (1974b) Examination of agonistic behavior by character analysis II: hermit crabs. Behaviour 49, 88-110.
Heimer, L. and Lohman, A.H.M. (1975) Anatomical methods for tracing connections in the central nervous system. In: Handbook of Psychobiology (M.S. Gazzaniga and C. Blakemore, eds.). Academic Press, New York, pp. 73-106.
Hendricks, D.E., Seay, B. and Barnes, B. (1975) The effects of the removal of dominant animals in a small group of Macaca fascicularis. J. Gen. Psychol. 92, 157-168.
Herkenham, M. and Nauta, W.J.H. (1977) Afferent connections of the habenular nuclei in the rat. A horseradish-peroxidase study with a note on the fiber-of-passage problem. J. comp. Neurol. 173, 123-146.
Hernández-Péon, R., O'Flaherty, J.J. and Mazzuchelli-O'Flaherty, A.L. (1967) Sleep and other behavioural effects induced by acetylcholinic stimulation of basal temporal cortex and striate structures. Brain Res. 4, 243-267.
Hinde, R.A. and Rowell, T.E. (1962) Communication by postures and facial expressions in the rhesus monkey (Macaca mulatta). Proc. zool. Soc. Lond. 138, 1-21.
Hinde, R.A. (1970) Animal Behaviour: A Synthesis of Ethology and Comparative Psychology. McGraw-Hill, New York.
Hinde, R.A. (1973) On the design of checksheets. Primates 14, 393-406.
Hong, J.S., Yang, H-Y.T., Racagni, G. and Costa, E. (1977) Projections of substance P containing neurons from neostriatum to substantia nigra. Brain Res. 122, 541-544.
Hoover, D.B., Muth, E.A. and Jacobowitz, D.J. (1978) A mapping of the distribution of acetylcholine, choline acetyltransferase and acetylcholinesterase in discrete areas of rat brain. Brain Res. 153, 295-306.
Hull, C.D., Buchwald, N.A. and Ling, G. (1967) Effects of direct cholinergic stimulation of forebrain structures. Brain Res. 6, 22-35.
Humphreys, P. (1974) Primate, Version 4: User's Manual. Brunel University Monograph 71/1, Uxbridge.
Hutt, S.J. and Hutt, C. (1970) Direct Observation and Measurement of Behaviour. Thomas, Springfield.
Jessell, T.M., Emson, P.C., Paxinos, G. and Cuello, A.C. (1978) Topographic projections of substance P and GABA-pathways in the striato- and pallido-nigral system: a biochemical and immunohistochemical study. Brain Res. 152, 487-498.
Jones, E.G., Coulter, J.D., Burton, H. and Porter, R. (1977) Cells of origin and terminal distribution of corticostriatal fibers arising in the sensory-motor cortex of monkeys. J. comp. Neurol. 173, 53-80.
Jung, R. and Hassler, R. (1960) The extrapyramidal motor system. In: Handbook of Physiology (J. Field, ed.) Vol. II/1. Am. Physiol. Soc., New York, pp. 863-927.

Kaada, B.R. (1972) Stimulation and regional ablation of the amygdaloid complex with reference to functional representation. In: The Neurobiology of the Amygdala (B.E. Eleftheriou, ed.). Plenum Press, New York, pp. 205-282.
Kalil, K. (1978) Patch-like termination of thalamic fibers in the putamen of the rhesus monkey: an auto-radiographic study. Brain Res. 140, 333-339.
Kalmus, H. (1969) Animal behaviour and theories of games and of languages. Anim. Behav. 17, 607-617.
Kanazawa, I., Emson, P.C. and Cuello, A.C. (1977) Evidence for the existence of substance P containing fibres in striatonigral and pallido-nigral pathways in rat brain. Brain Res. 119, 447-453.
Kemp, J. and Powell, T.P.S. (1971) The connexions of the striatum and globus pallidus: synthesis and speculation. Phil. Trans. R. Soc. Lond. B. 262, 441-457.
Kim, R., Katsuma, N., Jayaraman, A. and Carpenter, M.B. (1976) Projections of the globus pallidus and adjacent structures: an autoradiographic study in the monkey. J. comp. Neurol. 169, 263-290.
Kirkby, R.J. (1969) Caudate nucleus lesions and perseverative behavior. Physiol. Behav. 4, 451-454.
Kirkby, R.J. (1973) Caudate nucleus and arousal in the rat. J. comp. Physiol. Psychol. 85, 82-96.
Kirkby, R.J. and Polgar, S. (1976) Caudate nucleus and active avoidance: a reply to Winocur. Physiol. Behav. 4, 135-136.
Kirkby, R.J. (1978) Dorsal but not ventral lesions of the caudate nucleus disrupt Hebb-Williams maze learning in the rat. Physiol. Behav. 20, 669-671.
Klemm, W.R. and Dreyfus, L.R. (1975) Septal- and caudate-induced behavioral inhibition in relation to hippocampal EEG of rabbits. Physiol. Behav. 15, 561-567.
Kling, A. (1972) Effects of amygdalectomy on social-affective behavior in nonhuman primates. In: The Neurobiology of the Amygdala (B.E. Eleftheriou, ed.). Plenum Press, New York, pp. 511-536.
Kling, A. and Steklis, H.D. (1976) A neural substrate for affiliative behavior in nonhuman primates. Brain Behav. Evol. 13, 216-238.
Kochen, M. and Levy, M.J. (1956) The logical nature of an action scheme. Behav. Sci. 1, 265-269.
Krippendorff, K. (1971) A calculus for disagreements: a categorical equivalence to variance analysis. Gen. Systems XVI, 187-203.
Kuhar, M.J. and Yamamura, H.I. (1976) Localization of cholinergic muscarinic receptors in rat brain by light microscopic radiography. Brain Res. 110, 229-243.
Künzle, H. (1975) Bilateral projections from precentral motor cortex to the putamen and other parts of the basal ganglia. An autoradiographic study in Macaca fascicularis. Brain Res. 88, 195-209.
Laursen, A.M. (1963) Corpus striatum. Acta Physiol. scand. 59, suppl. 211.
Leger, D.W. (1977) An empirical evaluation of instantaneous and one-zero sampling of chimpansee behaviour. Primates 18, 387-393.

Lehman, M.N. and Adams, D.B. (1977) A statistical and motivational analysis of the social behaviors in the male laboratory rat. Behaviour 61, 238-275.
Lloyd, K. (1975) Special chemistry of the basal ganglia I. Monoamines. II. Distribution of acetylcholine, choline acetyltransferase and acetylcholinesterase. Pharmac. Therap. B. 1, 49-77.
Mackay, D.M. (1972) Formal analysis of communicative processes. In: Non Verbal Communication (R.A. Hinde, ed.). Cambridge University Press, Cambridge, pp. 3-25.
MacLean, P.D. (1978) Effects of lesion of globus pallidus on species-typical display behavior of squirrel monkeys. Brain Res. 149, 175-196.
Macrae, A.W. (1971) On calculating unbiased information measures. Psychol. Bull. 75, 270-277.
Marko, H. (1966) Die Theorie der bidirektionalen Kommunikation und ihre Anwendung auf die Nachrichtenübermittlung zwischen Menschen (subjektive Information). Kybernetik 3, 128-136.
Marko, H. (1973) The bidirectional communication theory: a generalization of information theory. IEEE Trans. Comm. Vol. Comm. 21, 1345-1351.
Maxim, P.E. (1976) An interval scale for studying and quantifying social relations in pairs of rhesus monkeys. J. exp. Ps. 105, 123-147.
Mayer, W. (1971) Gruppenverhalten von Totenkopfaffen unter besonderer Berücksichtigung der Kommunikationstheorie. Kybernetik 8, 59-68.
Mayhew, B.H., Gray, L.N. and Mayhew, M.L. (1971) The behaviour of interaction systems. Mathematical models of structure in interaction sequences. Gen. Syst. 16, 13-29.
McDowell, F. and Barbeau, A. (1974) Second Canadian-American Conference on Parkinson's Disease, Advances in Neurology Vol. 5. Raven Press, New York.
McGeer, E.G., Fibiger, H.C., McGeer, P.L. and Brooke, S. (1973) Temporal changes in amine synthesizing enzymes of rat extra pyramidal structures after hemitransection or 6-hydroxydopamine administration. Brain Res. 52, 289-300.
McGeer, E.P., McGeer, P.L. and Singh, K. (1978) Kainate-induced degeneration of neostriatal neurons: dependency upon corticostriatal tract. Brain Res. 139, 381-383.
McGeer, P.L., McGeer, E.G., Singh, V.K. and Chase, W.H. (1974) Choline acetyltransferase localization in the central nervous system by immunohistochemistry. Brain Res. 81, 373-379.
McGeer, P.L., McGeer, E.G., Scherer, U. and Singh, K. (1977) A glutamatergic corticostriatal path? Brain Res. 128, 369-373.
McGill, W.J. (1954) Multivariate information transmission. Psychometrika 19, 97-116.
McGill, W.J. (1955) Isomorphism in statistical analysis. In: Information Theory in Psychology (H. Quastler, ed.). Free Press, Glencoe Ill., pp. 56-70.
Mehler, W.R. and Nauta, W.J.H. (1974) Connections of the basal ganglia and of the cerebellum. Confin. Neurol. 36, 205-222.

Mettler, F.A. (1967) Cortical subcortical relations in abnormal motor functions. In: Neurophysiological Basis of Normal and Abnormal Motor Activity (M.D. Yahr and D.P. Purpura, eds.). Raven Press, New York, pp. 445-497.
Mettler, F.A. (1968) Anatomy of the basal ganglia. In: Handbook of Clinical Neurology Vol. 6: Diseases of the Basal Ganglia (P.J. Vinken and G.W. de Bruyn, eds.). North Holland Publishing Company, Amsterdam, pp. 1-35.
Metz, H. (1974) Stochastic models for the temporal fine structure of behaviour sequences. In: Motivational Control Systems Analysis (D. McFarland, ed.). Academic Press, London, pp. 5-86.
Miller, G.A., Galanter, E. and Pribram, K.H. (1960) Plans and the Structure of Behaviour. Holt, Rinehart & Winston, New York.
Miller, G.A. and Chomsky, N. (1963) Finitary models of language users. In: Handbook of Mathematical Psychology (R.D. Luce, R.R. Bush and E. Galanter, eds.) Vol. 2. Wiley and Sons, New York, pp. 419-492.
Miller, J.J., Richardson, T.L., Fibiger, H.C. and McLennan, H. (1975) Anatomical and electrophysiological identification of a projection from the mesencephalic raphe to the caudate-putamen in the rat. Brain Res. 97, 133-138.
Moles, A. (1963) Animal language and information theory. In: Acoustic Behaviour of Animals (R.G. Busnel, ed.). Elsevier Publishing Company, Amsterdam, pp. 112-131.
Morgan, B.J.T., Simpson, M.J.A., Hanby, J.P. and Hall-Craggs, J.H. (1976) Visualizing interaction and sequential data in animal behaviour: theory and application of cluster-analysis methods. Behaviour 56, 1-43.
Morley, B.J., Lorden, J.F., Brown, G.B., Kemp, G.E. and Bradley, R.J. (1977) Regional distribution of nicotinic acetylcholine receptor in rat brain. Brain Res. 139, 161-166.
Murphey, D.L. and Dill, R.E. (1972) Chemical stimulation of discrete brain loci as a method of producing dyskinesia models in primates. Exp. Neurol. 34, 244-254.
Myers, R.O. (1974) Handbook of Drug and Chemical Stimulation of the Brain, Behavioral, Pharmacological and Physiological Aspects. Van Nostrand Reinhold Company, New York.
Nagy, J. and Decsi. L. (1976) Effect of some intracerebrally administered drugs on a conditioned reflex in the cat. Physiol. Behav. 16, 21-25.
Neafsey, E.J., Hull, C.D. and Buchwald, N.A. (1978) Preparation for movement in the cat II. Unit activity in the basal ganglia and thalamus. Electroencephal. Clin. Neurophysiol. 44, 714-723.
Neill, D.B. (1976) Frontal-striatal control of behavioral inhibition in the rat. Brain Res. 105, 89-103.
Neill, D.B., Peay, L.A. and Gold, M.S. (1978) Identification of a subregion within rat neostriatum for the dopaminergic modulation of lateral hypothalamic self-stimulation. Brain Res. 153, 515-528.
Nemetz, T. (1972) On the experimental determination of the entropy. Kybernetik 10, 137-139.

Newtson, D. (1976) Foundations of attribution: the perception of ongoing behavior. In: New Directions in Attribute Research (J.H. Harvey, W.J. Ickes and R.F. Kidd, eds.) Vol. I. Lawrence Erlbaum, Hillsdale New Jersey, pp. 223-247.
Nieuwenhuys, R. (1977) Aspects of the morphology of the striatum. In: Psychobiology of the Striatum (A.R. Cools, A.H.M. Lohman and J.H.L. van den Bercken, eds.). North Holland Publishing Company, Amsterdam, pp. 1-20.
Norcross, K. and Spehlmann, R. (1978) A quantitative analysis of the excitatory and depressant effect of dopamine on the firing of caudatal neurons: electrophysiological support for the existence of two distinct dopamine-sensitive receptors. Brain Res. 156, 168-174.
Oberg, R.G.E. and Divac, I. (1975) Dissociative effects of selective lesions in the caudate nucleus of cats and rats. Acta Neurol. Exp. 35, 647-659.
Olivier, A., Parent, A., Simard, H. and Poirier, L.J. (1970) Cholinesterasic striatopallidal and striatonigral efferents in the cat and the monkey. Brain Res. 18, 273-282.
Olmstead, C.E., Villablanca, J.R., Marcus, R.J. and Avery, D.L. (1976) Effects of caudate nuclei or frontal cortex ablations in cats IV. Bar pressing, maze learning and performance. Exp. Neurol. 53, 670-693.
Pasik, P., Pasik, T. and DiFiglia, M. (1976) Quantitative aspects of neuronal organization in the neostriatum of the Macacaque monkey. In: The Basal Ganglia (M.D. Yahr, ed.). Raven Press, New York, pp. 57-90.
Pasik, P., Pasik, T. and DiFiglia, M. (1979) Internal structure of the neostriatum. In: Proceedings Workshop "The Neostriatum", April 16-20, 1978 (I. Divac, ed.). Plenum Press, London, in press.
Perachio, A.A. and Alexander, M. (1975) The neural bases of aggression and sexual behavior in the rhesus monkey. In: The Rhesus Monkey (G. Bourne, ed.) Vol. I. Academic Press, New York, pp. 382-409.
Pike, K.L. (1957) Towards a theory of the structure of human behavior. Gen. Syst. 2, 135-141.
Poirier, F.E. and Smith, E.O. (1974) The crab-eating macaques (macaca fascicularis) of Angani Island, Palau, Micronesia. Folia Primatol. 22, 258-306.
Poirier, L.J., Langelier, P., Bédard, P., Boucher, R., Carochelle, L., Parent, A. and Roberge, A.G. (1974) Dopaminergic and cholinergic mechanisms in relation to postural tremor in the monkey and circling movements in the cat. In: Advances in Neurology (F. McDowell and A. Barbeau, eds.) Vol. 5. Raven Press, New York, pp. 5-10.
Potegal, M. (1969) Role of the caudate nucleus in spatial orientation of rats. J. comp. Physiol. Psychol. 69, 756-764.
Potegal, M. (1972) The caudate nucleus egocentric localization system. Acta Neurobiol. Exp. 32, 479-494.
Powers, W.T. (1978) Quantitative analysis of purposive systems: some spadework at the foundation of scientific psychology. Ps. Rev. 85, 417-435.

Prado-Alcala, R.A., Grinberg-Zylberbaum, J., Alvarez-Leefmans, J., Gomez, A., Singer, S. and Brust-Carmona, H. (1972) A possible caudate cholinergic mechanism in two instrumental conditioned responses. Psychopharmacologia (Berl.) 25, 339-346.

Purpura, D.P. (1976) Physiological organization of the basal ganglia. In: The Basal Ganglia (M.D. Yahr, ed.). Raven Press, New York, pp. 91-114.

Purton, A.C. (1978) Ethological categories of behaviour and some consequences of their conflation. Anim. Behav. 26, 653-670.

Quastler, H. (1955) Information Theory in Psychology. Free Press, Glencoe Ill.

Racagni, G., Bruno, F., Cattabeni, F., Maggi, A., Di Gicelio, A.M., Parenti, M. and Gropetti, A. (1977) Functional interaction between rat substantia nigra and striatum: GABA- and dopamine interaction. Brain Res. 134, 353-358.

Redgrave, P. (1978) Modulation of intracranial self-stimulation behaviour by local perfusions of dopamine, noradrenaline and serotonin within the caudate nucleus and nucleus accumbens. Brain Res. 155, 277-295.

Redican, W.K. (1975) Facial expressions in nonhuman primates. In: Primate Behavior, Developments in Field and Laboratory Research (L.A. Rosenblum, ed.) Vol. 4. Academic Press, New York, pp. 104-194.

Reynolds, V. (1976) The origins of a behavioural vocabulary: the case of the rhesus monkey. J. Theory soc. Behav. 6, 105-142.

Roosen-Runge, P.H. (1966) Toward a theory of parts and wholes: an algebraic approach. Gen. Syst. 11, 13-18.

Ross, J. (1962) Informational coverage and correlational analysis. Psychometrika 27, 297-306.

Rosvold, H.E. and Delgado, J.M.R. (1963) The effect on delayed alternation performance of stimulating or destroying electrically structures within the frontal lobes of the monkey's brain. J. comp. Physiol. Psychol. 49, 365-392.

Rosvold, H.E. (1968) The prefrontal cortex and caudate nucleus: a system for effecting correction in response mechanisms. In: Mind as a Tissue (C. Rupp, ed.). Hoeber, New York, pp. 21-38.

Rowell, T.E. and Hinde, R.A. (1962) Vocal communication by the rhesus monkey (macaca mulatta). Proc. zool. Soc. Lond. 138, 279-294.

Royce, G.J. (1978a) Autoradiographic evidence for a discontinuous projection to the caudate nucleus from the centromedian nucleus in the cat. Brain Res. 146, 145-150.

Royce, G.J. (1978b) Cells of origin of subcortical afferent to the caudate nucleus: a horseradish peroxidase study in the cat. Brain Res. 153, 465-475.

Russell, W.M.S., Mead, A.P. and Hayes, J.S. (1954) A basis for the quantitative study of the structure of behaviour. Behaviour 6, 154.

Samanin, R., Quattrone, A., Peri, G., Ladinsky, H. and Consolo, S. (1978) Evidence of an interaction between serotonergic and cholinergic neurons in the corpus striatum and hippocampus of the rat brain. Brain Res. 151, 73-82.

Scally, M.C., Ulus, I.H., Wartman, R.J. and Pettibone, D.J. (1978) Regional distribution of neurotransmitter synthesizing enzymes and substance P within the rat corpus striatum. Brain Res. 143, 556-560.
Schank, R.C. (1972) Conceptual dependency theory: a theory of natural language understanding. Cogn. Ps. 3, 552-631.
Schank, R.C. and Abelson, R.P. (1977) Scripts, Plans, Goals and Understanding. An Inquiry into Human Knowledge Structures. Lawrence Erlbaum, Hillsdale New Jersey.
Schiff, B.B. and Carter, D. (1977) Long-term effects of caudate nucleus lesions on body weight in the rat. Physiol. Behav. 18, 375-379.
Shanta, T.R., Manocha, S.L. and Bourne, G.H. (1968) A Stereotaxic Atlas of the Java Monkey Brain. Karger, Basel.
Shapiro, D.Y. and Altham, P.M.E. (1978) Testing assumptions of data selection in focal animal sampling. Behaviour 62, 115-133.
Shirek-Ellefson, J. (1967) Visual Communication in Macaca Irus. Ph.D. Thesis, University of California, Berkeley. University Microfilms Inc., Ann Arbor Michigan.
Sibly, R. and McFarland, D. (1976) On the fitness of behavior sequences. The American Naturalist 110, 601-617.
Siegel, S. (1956) Non-parametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.
Simke, J.P. and Saelen, J.K. (1977) Evidence for a cholinergic fiber tract connecting the thalamus with the head of the striatum of the rat. Brain Res. 125, 487-495.
Simpson, M.J.A. and Simpson, A.E. (1977) One-zero and scan methods for sampling behaviour. Anim. Behav. 25, 726-731.
Slater, P.J.B. (1973) Describing sequences of behaviour. In: Perspectives in Ethology (P.P.G. Bateson and P.H. Klopfer, eds.). Plenum Press, New York, pp. 131-153.
Slater, P.J.B. (1978) Data collection. In: Quantitative Ethology (P.W. Colgan, ed.). Wiley, New York, pp. 7-24.
Sneath, P.H. and Sokal, R.R. (1973) Numerical Taxonomy. The Principles and Practice of Numerical Classification. Freeman, San Francisco.
Sockza, L. (1974) Ethologie sociale et sociométrie: analyse de la structure d'un groupe de singes crabiers (macaca fascicularis = irus) en captivité. Behaviour 50, 254-269.
Soltysik, S., Hull, C.P., Buchwald, N.A. and Fekete, T. (1975) Single unit activity in basal ganglia of monkeys during performance of a delayed response task. Electroencephal. Clin. Neurophysiol. 39, 65-78.
Steinberg, J.B. and Conant, J.R. (1974) An informational analysis of the intermale behaviour of the grasshopper Chortophaga viridifasciata. Anim. Behav. 22, 617-627.
Steinberg, J.B. (1977) Information theory as an ethological tool. In: Quantitative Methods in the Study of Animal Behavior (B.A. Hazlett, ed.). Academic Press, New York, pp. 47-74.
Stephenson, G.R., Smith, D.P.B. and Roberts, T.W. (1975) The SSR system: an open format event recording system with computerized transcription. Behav. Res. Meth. & Instr. 7, 497-515.

Stevens, J.R. and MacLean, P.D. (1961) Stimulation of caudate nucleus. Behavioral effects of chemical and electrical excitation. Arch. Neurol. (Chic.) 4, 47-54.
Taylor, G., Stynes, A.J., Kaufman, I.C. and Rock, K.C. (1975) A monkeyputer for automatic behavior scoring. Biom. Sci. Instr., 169-174.
Tembrock, G. (1973) Grundrisz der Verhaltenswissenschaften. G. Fischer Verlag, Stuttgart.
Ternaux, J.P., Héry, F., Bourgoin, S., Adrien, J., Glowinski, J. and Hamar, M. (1977) The topographical distribution of serotonergic terminals in the neostriatum of the rat and the caudate nucleus of the cat. Brain Res. 121, 311-326.
Teuber, H.L. (1976) Complex functions of basal ganglia. In: The Basal Ganglia (M.D. Yahr, ed.). Raven Press, New York, pp. 151-168.
Thomas, R.K. and Hill, A.S. (1973) The caudate nucleus and avoidance learning: a re-evaluation. Bull. Psychon. Soc. 1, 346-348.
Thompson, N.S. (1967) Some variables affecting the behaviour of Irus macaques in dyadic encounters. Anim. Behav. 15, 307-311.
Thompson, N.S. (1969) The motivations underlying social structure in Macaca Irus. Anim. Behav. 17, 459-467.
Toda, M. and Shuford, E.H. (1965) Logic of systems: introduction to a formal theory of structure. Gen. Syst. 10, 3-27.
Ursin, H., Sundberg, H. and Menaker, S. (1969) Habituation of the orienting response elicited by stimulation of the caudate nucleus in the cat. Neuropsychol. 7, 313-318.
Van den Bercken, J.H.L. and Cools, A.R. (1979) Role of the neostriatum in the initiation, continuation and termination of behaviour. Appl. Neurophysiol. 42, 106-108.
Van den Bercken, J.H.L. and Cools, A.R. (1980a) Information statistical analysis of social interaction and communication: an analysis of variance approach. Anim. Behav., in press.
Van den Bercken, J.H.L. and Cools, A.R. (1980b) Information statistical analysis of factors determining ongoing behaviour and social interaction in Java monkeys (Macaca fascicularis). Anim. Behav., in press.
Van den Bercken, J.H.L. and Cools, A.R. (submitted) Evidence for a role of the caudate nucleus in the sequential organization of behaviour.
Van Hooff, J.A.R.A.M. (1962) Facial expressions in higher primates. Symp. zool. Soc. Lond. 8, 97-125.
Van Hooff, J.A.R.A.M. (1967) The facial display of the catarrhine monkeys and apes. In: Primate Ethology (D. Morris, ed.). Weidenfeld and Nicolson, London, pp. 7-68.
Villablanca, J.R. and Marcus, R.J. (1975) The basal ganglia. A brief review and interpretation. Acta Neurol. Latinoamer. 21, 157-183.
Villablanca, J.R., Marcus, R.J. and Olmstead, C.E. (1976a) Effects of caudate nuclei or frontal cortical ablations in cats I. Neurology and gross behavior. Exp. Neurol. 52, 389-430.

Villablanca, J.R., Marcus, R.J. and Olmstead, C.E. (1976b) Effects of caudate nuclei or frontal cortex ablations in cats II. Sleep-wakefulness, EEG, and motor activity. Exp. Neurol. 53, 31-50.
Villablanca, J.R., Marcus, R.J., Olmstead, C.E. and Avery, D.L. (1976c) Effects of caudate nuclei or frontal cortex ablations in cats III. Recovery of limb placing reactions, including observations in hemispherectomized animals. Exp. Neurol. 53, 289-303.
Vogt, M. (1975) Release of putative transmitters from the corpus striatum. Pharmac. Therap. B. 1, 39-47.
Vosu, M. and Wise, R.A. (1975) Cholinergic seizure kindling in the rat: comparison of caudate amygdala and hippocampus. Behav. Biol. 13, 491-495.
Vowles, D.M. (1975) An introduction to neuroethology. In: Methods in Brain Research (P.B. Bradley, ed.). Wiley, New York, pp. 475-530.
Ward, A.A., jr. (1968) The function of the basal ganglia. In: Handbook of Clinical Neurology (P.J. Vinken en G.W. de Bruyn, eds.) Vol. 6: Diseases of the Basal Ganglia. North Holland Publishing Company, Amsterdam, pp. 90-115.
Waser, P.G. (1975) Cholinergic Mechanisms. Raven Press, New York.
Watanabe, S. (1960) Information-theoretical analysis of multivariate correlation. IBM Journal Res. Dev., 66-82.
Webster, W.G. (1973) Assumptions, conceptualizations, and the search for the functions of the brain. Physiol. Psychol. 1, 346-350.
Webster, K.E. (1975) The basal ganglia. Proc. Royal Soc. Med. 68, 203-210.
Welling, F. (1977) De Java-aap (Macaca fascicularis, Raffles 1821): algemene gegevens en het gedragsreperotire. Nijmegen, Katholieke Universiteit, vakgroep Vergelijkende en Fysiologische Psychologie.
Westman, R.S. (1977) Environmental languages and the functional bases of animal behavior. In: Quantitative Methods in the Study of Animal Behavior (B.A. Hazlett, ed.). Academic Press, New York, pp. 145-201.
Wilburn, M.W. and Kesner, R.P. (1974) Effects of caudate nucleus stimulation upon initiation and performance of a complex motor task. Exp. Neurol. 45, 61-71.
Wilson, E.O. (1975) Sociobiology. The New Synthesis. Belknap Press of Harvard University Press, Cambridge Mass.
Winocur, G. and Mills, J.A. (1969) Effects of caudate lesions in avoidance behaviour in rats. J. comp. Physiol. Psychol. 68, 552-557.
Winocur, G. (1974) Functional dissociation within the caudate nucleus of rats. J. comp. Physiol. Psychol. 86, 432-439.
Wright, H.F. (1967) Recording and Analyzing Child Behavior. Harper and Row, New York.
Yahr, M.D. (1976) The Basal Ganglia. Raven Press, New York.
Yamamura, H.I., Kuhar, M.J., Greenberg, D. and Snyder, S. (1974) Muscarinic cholinergic receptor binding: regional distribution in monkey brain. Brain Res. 66, 541-546.

Yeterian, E.H. and van Hoesen, G.W. (1978) Cortico-striate projections in the rhesus monkey: the organization of certain cortico-caudate connections. Brain Res. 139, 43-63.
Zagrodka, J. and Fonberg, E. (1978) Predatory versus alimentary behaviour after amygdala lesions in cats. Physiol. Behav. 20, 523-531.
Zülch, K.J. (1976) A critical appraisal of "Lokalisationslehre" in the brain. Naturwissenschaften 63, 255-265.

Addendum

Gottman, J.M. and Notarius, C. (1978) Sequential analysis of observational data using Markov chains. In: Single Subject Research - Strategies for Evaluating Change (Th.R. Kratochwill, ed.). Academic Press, New York, pp. 237-286.
Herz, M.J., Wyers, E.J. and Peeke, H.V.S. (1975) Caudate stimulation and the production of retrograde amnesia. In: Subcortical Mechanisms Sensorimotor Activities (T.L. Frigyesi, ed.). Huber, Bern, pp. 193-215.
Losey, G.S. jr. (1978) Information theory and communication. In: Quantitative Ethology (P.W. Colgan, ed.). Wiley and Sons, New York, pp. 43-78.

Velen hebben op enigerlei wijze bijgedragen aan de totstandkoming van dit proefschrift; hen dank ik graag voor de geboden medewerking.

In het bijzonder ben ik erkentelijk voor de prettige en werkzame sfeer binnen de sectie Psychofarmacologie van het Farmacologisch Laboratorium. Ook de leden van de BION-werkgemeenschap voor Ethologie, m.n. van de projektgroepen Gedragssystemen, Gedragsmechanismen en Primatengedrag, vormden vaak een welwillend klankbord: van hen kreeg ik menig waardevolle suggestie. De plezierige contacten en stimulerende discussies met de leden van de vakgroep Vergelijkende en Fysiologische Psychologie waren ook na mijn studententijd een bron van inspiratie voor veel van de ideeën die ten grondslag liggen aan dit proefschrift.

Technische assistentie bij het uitvoeren van de experimenten werd op bekwame wijze verleend door Dik Heeren, Huub Geurts en Frans de Boer van de Technische Dienst van de Faculteit der Wiskunde en Natuurwetenschappen en Jan Jansen van het Farmacologisch Laboratorium. Hulp bij de operatie van de proefdieren werd met veel inzet gegeven door Hendrik-Jan Janssen en Fred Philipsen van het Centraal Dierenlaboratorium; de huisvesting en verzorging van de dieren was in voortreffelijke handen bij de heren A. Peters en P. Spaan en hun medewerkers, eveneens van het Centraal Dierenlaboratorium; ook voor andere aspecten van het onderzoek bleek de prettige samenwerking met het Centraal Dierenlaboratorium vruchtbaar.

Bij het observeren en het uitwerken van de gegevens was Wiel Honig menigmaal behulpzaam.

Het moeizame werk van het verzamelen van de relevante literatuur werd aanmerkelijk verlicht door de efficiënte hulp van de heer E. de Graaf en zijn medewerkers en van Mevr. N. Latupeirissa-Post.

Van hen die de inhoud van het manuscript bestudeerden en op creatieve wijze van commentaar voorzagen, wil ik met name Rik Broekkamp en Paul van Dongen bedanken.

Donald Hatch nam de Engelse tekst nauwgezet door en gaf menige verfraaiing in de formulering aan; daarvan heb ik graag gebruik gemaakt.

Tenslotte wil ik ook Margot Klumpkens-Janssen danken voor de onvermoeibare en vaardige wijze waarop zij het manuscript vorm wist te geven.

John H.L. van den Bercken:
geboren 14 maart 1945 te Horst; eindexamen gymnasium-α in 1963; van 1968 tot 1971 studie in de psychologie te Utrecht (kandidaatsexamen); van 1971 tot 1974 doctoraalstudie in de psychologie te Nijmegen aan de vakgroep Vergelijkende en Fysiologische Psychologie en aan de vakgroep Mathematische Psychologie en Statistiek; vanaf februari 1975 werkzaam bij de sectie Psychofarmacologie van het Farmacologisch Instituut te Nijmegen (tot 1978 in dienst van de Nederlandse Organisatie voor Zuiver-Wetenschappelijk Onderzoek, ZWO, te Den Haag). Sinds oktober 1979 als methodoloog werkzaam bij de sectie Research van de vakgroep Orthopedagogiek te Nijmegen.

Uit gezamenlijk onderzoek zijn de volgende publicaties voortgekomen:

Cools, A.R. and Van den Bercken, J.H.L. (1977) Cerebral organization of behaviour and the neostriatal function. In: Psychobiology of the Striatum (A.R. Cools, A.H.M. Lohman and J.H.L. van den Bercken, eds.) North Holland Publishing Company, Amsterdam, pp. 119-140.

Van den Bercken, J.H.L. and Cools, A.R. (1979): Role of the neostriatum in the initiation, continuating and termination of behaviour. Appl. Neurophysiol. 42, 106-108.

Van den Bercken, J.H.L. and Cools, A.R. (1980a) Information statistical analysis of social interaction and communication: an analysis of variance approach. Anim. Behav., in press.

Van den Bercken, J.H.L. and Cools, A.R. (1980b) Information statistical analysis of factors determining ongoing behaviour and social interaction in Java monkeys (Macaca fascicularis). Anim. Behav., in press.

Van den Bercken, J.H.L. and Cools, A.R. (submitted) Evidence for a role of the caudate nucleus in the sequential organization of behaviour.

Van den Bercken, J.H.L. en Cools, A.R. (1976, 1977) Hersen-injecties en beïnvloeding van het sociale gedrag van Java-apen: illustratie van een neurobiologisch onderzoek. Biotechniek 15, 192-196 en 16, 1-10.

Van den Bercken, J.H.L. (in druk) De nucleus caudatus en sociaal gedrag bij Java-apen. Ned. Vakblad v. Biologen.

STELLINGEN

1

Gedrag dat waargenomen kan worden in ethologische, d.i. min of meer vrije en natuurlijke, situaties is niet gemakkelijker te begrijpen dan gedrag dat optreedt in psychologische, d.i. experimenteel beperkte test-condities; het interpretatieprobleem in het eerste geval is niet kleiner dan het validiteitsprobleem in het andere geval.

Dit proefschrift

2

Het informatie-theoretische principe dat iets wat zelden optreedt zeer informatief is, betekent voor de ethologie dat elk bitje informatie gekocht moet worden met vele uren observatie.

Dit proefschrift

3

Wanneer men bij experimentele ingrepen in de hersenen, met name bij chemische en electrische stimulatie, wacht tot een drempel voor onmiddellijk waarneembare gedragseffecten bereikt is, mist men veelal subtiele veranderingen in de organisatie van gedrag die vóór die drempel kunnen optreden.

Dit proefschrift

4

De redenen waarom attributie een geldige basis levert voor het verklaren en begrijpen van andermans gedrag zijn ook van toepassing bij het verklaren en begrijpen van diergedrag.

W.H. Thorpe, 1966: Ethology and consciousness. in: J.C. Eccles (ed.): Brain and Consciousness, Berlin, Springer, pp. 470-505.
R. Harré and P.F. Secord, 1972: The Explanation of Social Behaviour, Oxford, Basil Blackwell.

5

De experimentele paradigmata voor respondent en operant conditioneren moeten primair geïnterpreteerd worden als vormen van patroonherkenning; als zodanig onderschatten ze de aanpassingscapaciteit van het lerend organisme.

D. Michie, 1974: Puzzle-learning versus game-learning in studies of behaviour. in: On Machine Intelligence, Edinburgh, U.P., pp. 21-30.

Er zijn voldoende aanwijzingen om het onderscheid tussen hypothese-gebruik en associatie-leren als verschillende strategieën voor het oplossen van problemen bij primaten niet te laten samenvallen met de indeling in mens-apen (apes) en apen (monkeys).

S.M. Essock-Vitale, 1978: Comparison of ape and monkey modes of problem solution, J. comp. Physiol. Psychol. 92, 942-957.

7

Pieper's definitie van "behavioral toxicity" als "failure to respond" of "a reduction in acquisition performance which is measured by a sequential learning task" is hoogst aanvechtbaar zowel om inhoudelijke als om methodologische redenen.

W.H. Pieper, 1977: Acute effects of stimulants and depressants on sequential learning in great apes. in: G.H. Bourne (ed.): Progress in Ape Research, New York, Academic Press, pp. 167-176.

8

Programmeren is meer dan alleen maar een technisch hulpmiddel voor een vlotte data-analyse; het is een model bij uitstek van de wetenschappelijke activiteit van de gedragsonderzoeker.

R. Cummins, 1976: Programs in the explanation of behaviour, Philos. of Science 54, 269-287.

9

Argumenten ten gunste van de "Mind-Brain Identity"-theorie zijn niet uit hun aard ook argumenten ten gunste van een wetenschapstheoretisch reductionisme.

H. Putnam, 1973: Reductionism and the nature of psychology, Cognition 2, 131-144.
J. Fodor, 1976: The Language of Thought. Hassocks, The Harvester Press.
M. Bunge, 1977: Emergence and the mind. Neuroscience 2, 501-509.

10

Als het verband tussen perceptie en werkelijkheid grotendeels beheerst en beperkt wordt door onze genen, dan is verscheidenheid in ideologie en methodologie even adaptief als genetische verscheidenheid.

D.L. Wilson, 1978: Neurobiology and epistemology, Fed. Proc. 37, 2275-2280.
P. Feyerabend, 1975: Against Method, London, NLB.

11

Het verschijnsel, dat men tijdens een droom beseft te dromen, is positief gecorreleerd met sociale perceptiviteit, met name voor paralinguistische informatie. - Het is jammer dat bij het huidige wetenschapsideaal van de psychologie zo'n feit ontoegankelijk is.

G. Westland, 1978: Current Crises of Psychology, London, Heinemann.

12

Onze hersenen hebben met computers in ieder geval gemeen dat de beschikbaarheid vaak zwaarder weegt dan de bezettingsgraad.

Vgl. Intermediair, 1979, nr. 24.